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A New Leaf Litter Toad of *Leptobrachella* Smith, 1925 (Anura, Megophryidae) from Sichuan Province, China with Supplementary Description of *L. oshanensis*

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Abstract A new species of the Asian leaf litter toad genus *Leptobrachella* is described from Sichuan Province, China. Molecular phylogenetic analyses based on mitochondrial and nuclear gene sequences clustered the new species as an independent clade nested into *L. oshanensis* species group. The new species could be distinguished from its congeners by a combination of following characters: body size moderate (25.8–32.6 mm in male, 33.7–34.1 mm in female); distinct black spots present on flanks; toes rudimentary webbed, with narrow lateral fringes, dermal ridges under toes interrupted at articulations; ventral belly cream white with variable brown specking; skin on dorsum relatively smooth with fine tiny granules or short ridges; iris copper above, silver bellow; greyish black patches on posterior thigh absent or small; spines on surface of chest absent in male during breeding season; nasals entirely or partially separated from sphenethmoid in male; dorsal surface of tadpoles semitransparent light brown, spots on tail absent, keratodont row formula I: 3+3(2+2)/2+2: I; calls simple, call series basically consist of repeated long calls, at dominant frequency (4831.9 ± 155.8) Hz and call duration (544.5 ± 146.8) ms. In addition, we made supplementary description on *L. oshanensis* including holotype, variations, tadpoles, skull and bioacoustics. Besides, this paper reports cases of femoral adipose glands in the genus *Leptobrachella* as first known sexual dimorphism skin glands for males of Megophryidae.

Keywords multiple data, new species, sympatric distribution, taxonomy

1. Introduction

The Asian leaf litter toad genus *Leptobrachella* Smith, 1925 (Anura, Megophryidae Bonaparte, 1850) is a group of morphologically conserved small toads associated with forest floor and rocky streams in hilly evergreen forest, and is widely distributed from southern China and Myanmar, through mainland Indochina to peninsular Malaysia and the island of Borneo (Rowley *et al.*, 2016, 2017; Frost, 2020). The taxa in this group had been classified into different genera, i.e., *Paramegophrys* Liu, 1964, *Carpophrys* Sichuan Biological Research Institute, 1977, *Leptolalax* Dubois, 1980, *Lalax* Delorme, Dubois, Grosjean and Ohler, 2006, and *Lalos* Dubois, Grosjean, Ohler, Adler and Zhao, 2010. Based on large-scale molecular phylogenetic analyses on this group, Chen *et al.* (2018) indicated that above genera names were synonymized with *Leptobrachella*. Currently, *Leptobrachella* contains 82 species, of which, as note, 49 species were described in the last decade (Frost, 2020). Yet, the species diversity in the genus has been underestimated, and many cryptic species were still proposed especially in populations of the species with wide distributional ranges (Chen *et al.*, 2018).

Leptobrachella oshanensis (Liu, 1950) has been recorded in

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Gansu, Sichuan, Chongqing, Guizhou, Hubei and Hunan provinces of China (Xiang *et al.*, 2008; Fei *et al.*, 2012, 2016). Chen *et al.* (2018) indicated that this widely distributed species should be a species complex containing some paraphyletic lineages and several cryptic species even in the type locality, Emei Mountain in Sichuan Province, China. Soon afterwards, five new species, i.e., *Leptobrachella bijie* Wang, Li, Li, Chen and Wang, 2019, *Leptobrachella purpuraventra* Wang, Li, Li, Chen and Wang, 2019, *Leptobrachella suiyangensis* Luo, Xiao, Gao and Zhou, 2020, *Leptobrachella chishuiensis* Li, Liu, Wei, and Wang, 2020, and *Leptobrachella wulingensis* Qian, Xiao, Cao, Xiao and Yang, 2020 were described from the populations that had been recognized as *L. oshanensis*.

In recent years, we collected a series of *Leptobrachella* specimens from Emei Mountain, Sichuan Province, China. Molecular phylogenetic analyses, morphological comparisons and bioacoustics data indicated that they belong to two species, i.e., *L. oshanensis* and an undescribed species. Herein we described the undescribed taxon as a new species.

2. Materials and Methods

2.1. Sampling A total of 21 samples of the undescribed species including two adult females, nine adult males and nine tadpoles and 23 samples of *L. oshanensis* including eleven tadpoles, two adult females and ten adult males were collected from Emei Mountain, Sichuan Province, China (Figure 1; Table 1). Taxonomic identification of tadpoles was confirmed by sequencing of 16S rRNA gene. After taking photographs, the toads and tadpoles were euthanized using isoflurane, and then the specimens were fixed in 75% ethanol. Tissue samples were taken and preserved separately in 95% ethanol prior to fixation. Specimens were deposited in Chengdu Institute of Biology, Chinese Academy of Sciences (CIB, CAS).

2.2 Molecular phylogenetic analyses Total DNA was extracted from the specimens collected in this study using a standard phenol-chloroform extraction protocol (Sambrook *et al.*, 1989). The mitochondrial 16S gene and nuclear gene RAG1 were sequenced. Primer sequences were retrieved from literatures for 16S (Simon *et al.*, 1994) and RAG1 (Fu *et al.*, 2007). PCR amplifications for 16S gene were performed in a 25 μL volume reaction with the following conditions: an initial denaturing step at 95 °C for 4 min; 36 cycles of denaturing at 95 °C for 40 s, annealing at 55 °C for 40 s and extending at 72 °C for 70 s, and a final extending step of 72 °C for 10 min. Amplifications of RAG1 gene were according to Mahony *et al.* (2017). PCR products were sequenced with both forward and reverse primers same as used in PCR. Sequencing was conducted using an ABI3730 automated DNA sequencer in Sangon Biotechnologies Co., Ltd. (Shanghai, China). New sequences were deposited in GenBank (for accession numbers see Table 1).

For phylogenetic comparisons, corresponding sequences of all *Leptobrachella* species were downloaded from GenBank

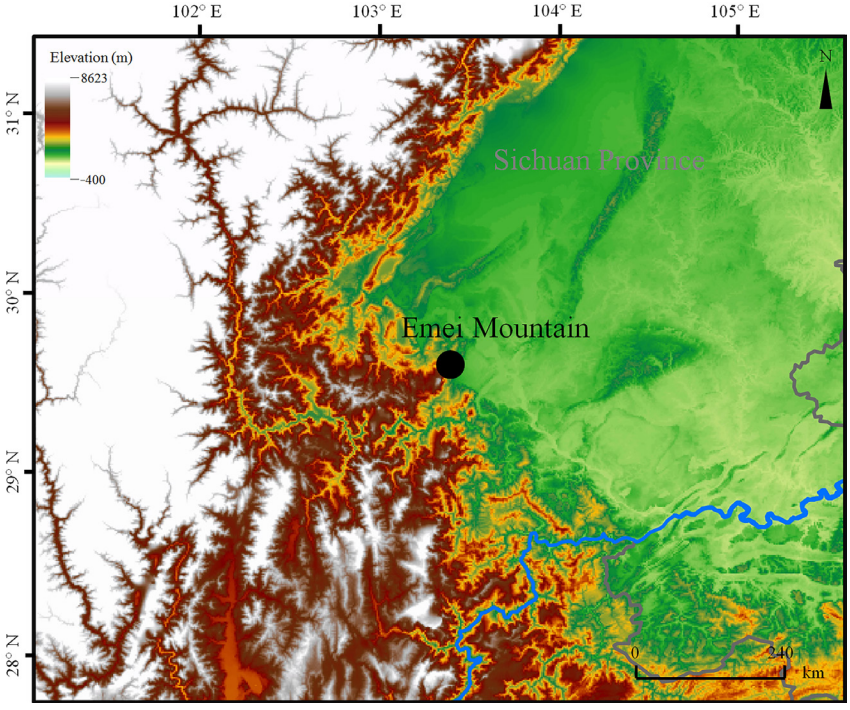

Figure 1 Location of the type locality of *Leptobrachella yeae* sp. nov. and *L. oshanensis*, Emei Mountain, Sichuan Province, China.

Table 1 Information for samples used in molecular phylogenetic analyses in this study.

ID	Species	Voucher	Locality	GenBank accession No.	
				16S	RAG1
1	*Leptobrachella yeae* sp. nov.	CIBEMS20190422HLJ1-3	Heilongjiang, Mount Emei, Sichuan, China	MT957002	/
2	*Leptobrachella yeae* sp. nov.	CIBEM1849	Changshouqiao, Mount Emei, Sichuan, China	MT957003	/
3	*Leptobrachella yeae* sp. nov.	CIBEMS20190422HLJ1-8	Heilongjiang, Mount Emei, Sichuan, China	MT957004	/
4	*Leptobrachella yeae* sp. nov.	CIBEM1867	Changshouqiao, Mount Emei, Sichuan, China	MT957005	MT975978
5	*Leptobrachella yeae* sp. nov.	CIBEMLGL19052104	Linggongli, Mount Emei, Sichuan, China	MT957006	MT975979
6	*Leptobrachella yeae* sp. nov.	CIBEM1844	Changshouqiao, Mount Emei, Sichuan, China	MT957007	/
7	*Leptobrachella yeae* sp. nov.	CIBSC072	Changshouqiao, Mount Emei, Sichuan, China	MT957008	/
8	*Leptobrachella yeae* sp. nov.	CIBSC070	Heilongjiang, Mount Emei, Sichuan, China	MT957009	/
9	*Leptobrachella yeae* sp. nov.	CIBEM1845	Changshouqiao, Mount Emei, Sichuan, China	MT957010	MT975977
10	*Leptobrachella yeae* sp. nov.	CIBEM1842	Changshouqiao, Mount Emei, Sichuan, China	MT957011	/
11	*Leptobrachella yeae* sp. nov.	CIBSC066	Heilongjiang, Mount Emei, Sichuan, China	MT957012	/
12	*Leptobrachella yeae* sp. nov.	CIBEM1841	Changshouqiao, Mount Emei, Sichuan, China	MT957013	/
13	*Leptobrachella yeae* sp. nov.	CIBEM1840	Changshouqiao, Mount Emei, Sichuan, China	MT957014	/
14	*Leptobrachella yeae* sp. nov.	CIBEMS20190422HLJ1-7	Heilongjiang, Mount Emei, Sichuan, China	MT957015	/
15	*Leptobrachella yeae* sp. nov.	CIBSC069	Heilongjiang, Mount Emei, Sichuan, China	MT957016	/
16	*Leptobrachella yeae* sp. nov.	CIBEMS20190422HLJ1-1	Heilongjiang, Mount Emei, Sichuan, China	MT957017	/
17	*Leptobrachella yeae* sp. nov.	CIBSC068	Heilongjiang, Mount Emei, Sichuan, China	MT957018	/
18	*Leptobrachella yeae* sp. nov.	CIBEMS20190422HLJ1-6	Heilongjiang, Mount Emei, Sichuan, China	MT957019	MT975975
19	*Leptobrachella yeae* sp. nov.	CIBSC071	Changshouqiao, Mount Emei, Sichuan, China	MT957020	/
20	*Leptobrachella yeae* sp. nov.	CIBEM1839	Changshouqiao, Mount Emei, Sichuan, China	MT957021	MT975976
21	*Leptobrachella yeae* sp. nov.	CIBEMS20190422HLJ2-1	Heilongjiang, Mount Emei, Sichuan, China	MT957022	MT975974
22	*L. alpina*	KIZ046816	Huangcaoling, Yunnan, China	MH055866	/
23	*L. purpurus*	SYS a006530	Yingjiang, Yunnan, China	MG520354	/
24	*L. suiyangensis*	GZNU20180606002	Suiyang, Guizhou, China	MK829648	/
25	*L. purpuraventra*	SYS a007284	Wujing Nature Reserve, Bijie, Guizhou, China	MK414524	/
26	*L. bijie*	SYS a007316	Zhaozishan Nature Reserve, Bijie, Guizhou, China	MK414535	/
27	*L. chishuiensis*	CIBCS20190518047	Chishui National Nature Reserve, Chishui, Guizhou, China	MT117053	/
28	*L. niveimontis*	KIZ015743	Daxueshan Nature Reserve, Yunnan, China	MH055877	/
29	*L. bourreti*	AMS R 177673	Lao Cai, Vietnam	KR018124	/
30	*L. wulingensis*	CSUFT 177	Tianquanshan Forest Park, Zhangjiajie, Hunan, China	MT530315	/
31	*L. oshanensis*	CIBEMS20190421BGS1	Baoguosi, Mount Emei, Sichuan, China	MT957023	MT975988
32	*L. oshanensis*	CIBEMS20190422SSG2-1	Shengshuige, Mount Emei, Sichuan, China	MT957024	/
33	*L. oshanensis*	CIBEMS20190422SSG1-4	Shengshuige, Mount Emei, Sichuan, China	MT957025	MT975985
34	*L. oshanensis*	CIBEMS20190422SSG3-2	Shengshuige, Mount Emei, Sichuan, China	MT957026	/
35	*L. oshanensis*	CIBEMS20190422HLJ1-4	Heilongjiang, Mount Emei, Sichuan, China	MT957027	MT975990
36	*L. oshanensis*	CIBEMS20190422SSG4-1	Shengshuige, Mount Emei, Sichuan, China	MT957028	/
37	*L. oshanensis*	CIBEMS20190422SSG1-2	Shengshuige, Mount Emei, Sichuan, China	MT957029	/
38	*L. oshanensis*	CIBEMS20190421SSG1-11	Shengshuige, Mount Emei, Sichuan, China	MT957030	/
39	*L. oshanensis*	CIBEMS20190421SSG1-10	Shengshuige, Mount Emei, Sichuan, China	MT957031	MT975983
40	*L. oshanensis*	CIBEMS20190422SSG1-3	Shengshuige, Mount Emei, Sichuan, China	MT957032	/
41	*L. oshanensis*	CIBEMS20190422HLJ1-2	Heilongjiang, Mount Emei, Sichuan, China	MT957033	MT975989
42	*L. oshanensis*	CIBSC064	Shengshuige, Mount Emei, Sichuan, China	MT957034	/
43	*L. oshanensis*	CIBSC063	Shengshuige, Mount Emei, Sichuan, China	MT957035	/
44	*L. oshanensis*	CIBEMS20190422SSG3-1	Shengshuige, Mount Emei, Sichuan, China	MT957036	MT975981
45	*L. oshanensis*	CIBEMS20190421BGS7	Baoguosi, Mount Emei, Sichuan, China	MT957037	MT975987
46	*L. oshanensis*	CIBEMS20190422SSG1-1	Shengshuige, Mount Emei, Sichuan, China	MT957038	MT975984
47	*L. oshanensis*	CIBEMS20190421SSG1-9	Shengshuige, Mount Emei, Sichuan, China	MT957039	MT975980
48	*L. oshanensis*	CIBEMS20190421SSG1-8	Shengshuige, Mount Emei, Sichuan, China	MT957040	MT975982
49	*L. oshanensis*	CIBSC062	Shengshuige, Mount Emei, Sichuan, China	MT957041	/
50	*L. oshanensis*	CIBEMS20190421BGS6	Baoguosi, Mount Emei, Sichuan, China	MT957042	MT975986
51	*L. oshanensis*	CIBEMS20190421BGS9	Baoguosi, Mount Emei, Sichuan, China	MT957043	/
52	*L. oshanensis*	CIBEMS20190421BGS8	Baoguosi, Mount Emei, Sichuan, China	MT957044	/
53	*L. oshanensis*	CIBEMS20190421BGS5	Baoguosi, Mount Emei, Sichuan, China	MT957045	/
54	*L. eos*	MNHN: 2004.0278	Phongsaly, Laos	JN848450	/
55	*L. tengchongensis*	SYS a004598	Tengchong, Yunnan, China	KU589209	/
56	*L. puhoatensis*	AMS:R184852	Pu Hoat Nature Reserve, Nghe An, Vietnam	KY849588	/
57	*L. namdongensis*	VNUF A.2017.37	Thanh Hoa, Vietnam	MK965389	/
58	*L. petrops*	AMS:R184826	Tuyen Quang, Vietnam	KY459997	/
59	*L. yingjiangensis*	SYS a006532	Yingjiang, Yunnan, China	MG520351	/
60	*L. khasiorum*	SDBDU 2009.329	East Khasi Hills, Meghalaya, India	KY022303	/
61	*L. liui*	SYS a001597	Wuyishan, Fujian, China	KM014547	/
62	*L. mangshanensis*	MSZTC201701	Mangshan, Hunan, China	MG132196	/
63	*L. laui*	SYS a001507	Wutongshan, Shenzhen, Guangdong, China	KM014544	/
64	*L. maoershanensis*	KIZ07614	Mao'er Shan, Guangxi, China	MH055927	MH056099
65	*L. yunkaiensis*	SYS a004664 / CIB107272	Dawuling Forest Station, Maoming, Guangdong, China	MH605585	/
66	*L. flaviglandulosa*	KIZ016072	Xiaoqiaogou Nature Reserve, Yunnan, China	MH055934	/
67	*L. sungi*	ROM 20236	Tam Dao, Vinh Phuc, Vietnam	MH055858	MH056104
68	*L. zhangyapingi*	KIZ07258	Pang Num Poo, Chiang Mai, Thailand	MH055864	/
69	*L. isos*	VNMN A 2015.4/AMS R 176480	Gia Lai, Vietnam	KT824769	/
70	*L. firthi*	AMS R 176524	Kon Tum, Vietnam	JQ739206	/
71	*L. minima*	KUHE:19201	Doi Suthep, Thailand	LC201981	/
72	*L. ventripunctata*	SYS a004536	Zhushihe, Yunnan, China	MH055831	/
73	*L. feii*	KIZ048893	Xiaoqiaogou Nature Reserve, Yunnan, China	MH055841	/
74	*L. aereus*	ZFMK 86362	U Bo, Quang Binh, Vietnam	JN848409	/

(Continued Table 1)

ID	Species	Voucher	Locality	GenBank accession No.	
				16S	RAG1
75	*L. wuhuangmontis*	SYS a003500 / CIB107274	Mount Wuhuang, Pubei, Guangxi, China	MH605581	/
76	*L. pluvialis*	MNHN:1999.5675	Mount Fan Si Pan, Lao Cai, Vietnam	JN848391	/
77	*L. shangsiensis*	NHMG1704002	Guangxi, China	MK095462	/
78	*L. nyx*	AMNH A163810	Ha Giang, Vietnam	DQ283381	/
79	*L. nahangensis*	ROM 7035	Na Hang Nature Reserve, Tuyen Quang, Vietnam	MH055853	/
80	*L. kalonensis*	IEBR A.2015.15	Binh Thuan, Vietnam	KR018114	/
81	*L. bidoupensis*	ZMMU-A-4797-01454	Bidoup-Nui Ba National Park, Lam Dong, Vietnam	MH055945	MH056110
82	*L. pallida*	UNS00510	Lam Dong, Vietnam	KR018112	/
83	*L. tadungensis*	UNS00515	Dak Nong, Vietnam	KR018121	/
84	*L. macrops*	IEBR A.2017.9	Mount Hon Den, Phu Yen, Vietnam	MG787990	/
85	*L. pyrrhops*	ZMMU ABV-00148	Loc Bao, Lam Dong, Vietnam	KP017575	/
86	*L. maculosa*	AMS R 177660	Ninh Thuan, Vietnam	KR018119	/
87	*L. melica*	MVZ 258197	Virachey National Park, Ratanakiri, Cambodia	HM133599	/
88	*L. applebyi*	AMS R171704	Song Thanh, Quang Nam, Vietnam	HM133598	/
89	*L. rowleyae*	ITBCZ 2783	Son Tra, Da Nang, Vietnam	MG682552	/
90	*L. ardens*	ZMMU-NAP-06099	Kon Ka Kinh National Park, Gia Lai, Vietnam	MH055949	MH056108
91	*L. tuberosa*	ZMMU-NAP-02275	Kon Ka Kinh National Park, Gia Lai, Vietnam	MH055959	MH056111
92	*L. croceus*	AMS R 173740	Kon Tum, Vietnam	MH055954	/
93	*L. botsfordi*	VNMN 03682	Fansipan, Lao Cai, Vietnam	MH055953	MH056089
94	*L. itiokai*	KUHE:55897	Mulu National Park, Sarawak, Borneo, Malaysia	LC137805	MH056120
95	*L. parva*	KUHE 55308	Mulu National Park, Sarawak, Borneo, Malaysia	LC056791	MH056121
96	*L. baluensis*	SP 21604	Tambunan, Sabah, Borneo, Malaysia	LC056792	/
97	*L. brevicrus*	KUHE 55844	Mulu National Park, Sarawak, Borneo, Malaysia	LC137807	/
98	*L. mjobergi*	KUHE 17064	Gading National Park, Sarawak, Borneo, Malaysia	LC056785	/
99	*L. juliandringi*	SRC 00230/KUHE 49815	Mulu National Park, Sarawak, Borneo, Malaysia	LC056779	/
100	*L. fuliginosus*	KUHE:20172	Thailand	LC201985	/
101	*L. melanoleuca*	KIZ018031	Kapoe, Ranong, Thailand	MH055967	MH056115
102	*L. sabahmontana*	BORNEENSIS 12632	Borneo, Malaysia	AB847551	/
103	*L. dringi*	KUHE 55610	Camp 4 of Gunung Mulu, Malaysia	AB847553	/
104	*L. picta*	UNIMAS 8705	Gunung Kinabalu National Park, Sabah, Malaysia	KJ831295	/
105	*L. fritinniens*	FMNH 244800	Danum Valley Field Center, Sabah, Malaysia	MH055971	MH056118
106	*L. hamidi*	KUHE:17545	Borneo, Malaysia	AB969286	/
107	*L. arayai*	BORNEEISIS 22931	Liwagu, Kinabalu, Borneo, Malaysia	AB847558	/
108	*L. melanoleuca*	KUHE:53227	Annah Rais, Padawan, Kuching Division, Sarawak, Malaysia	AB969289	/
109	*L. gracilis*	FMNH 273682	Bukit Kana, Sarawak, Malaysia	MH055972	MH056117
110	*L. maura*	SP 21450	Kinabalu, Sabah, Malaysia	AB847559	/
111	*L. solus*	KU RMB20973	Gunung Stong, Kelantan, Malaysia	MH055973	MH056119
112	*L. heteropus*	KUHE 15487	Larut, Peninsular, Malaysia	AB530453	/
113	*L. kecil*	KUHE:52440	Malaysia	LC202004	/
114	*L. kajangensis*	LSUHC:4439	Tioman, Malaysia	LC202002	/
115	*Leptobrachium huashen*	KIZ049025	Yunnan, China	KX811931	MH056122
116	*Megophrys glandulosa*	KIZ048439	Yunnan, China	KX811762	MH056125

especially for their holotypes and/or topotypes for which comparable sequences were available (for accession numbers see Table 1). Corresponding sequences of one *Megophrys glandulosa* and one *Leptobrachium huashen* were downloaded from GenBank (for accession numbers see Table 1) and were used as outgroups according to previous studies (Chen *et al.*, 2018).

Sequences were assembled and aligned using BioEdit v. 7.0.9.0 (Hall, 1999) with default settings, and were further revised manually when necessary. To avoid bias in alignments, GBLOCKS v. 0.91.b (Castresana, 2000) with default settings was used to extract regions of defined sequence conservation from the length-variable 16S fragments. The protein-coding gene RAG1 sequences were translated to amino acid sequences in MEGA v. 7.0 (Kumar *et al.*, 2016), adjusted for open reading frames, and checked to ensure absence of premature stop codons. No-sequenced fragments were treated as missing data.

Phylogenetic analyses were conducted on each gene using maximum likelihood (ML) and Bayesian Inference (BI) methods, implemented in PhyML v. 3.0 (Guindon *et al.*, 2010) and MrBayes v. 3.2 (Ronquist *et al.*, 2012), respectively. For the phylogenetic analyses, the best evolutionary model was selected based on the Bayesian Inference Criteria (BIC) using jModelTest v. 2.1.3 (Darriba *et al.*, 2012). The analyses selected GTR + I + G model for 16S gene, and K80 + I + G for RGA1 gene. For the ML tree, branch supports were drawn from 10000 non-parametric bootstrap replicates. In BI analyses, the parameters for each partition were unlinked, and branch lengths were allowed to vary proportionately across partitions. Two runs each with four Markov chains were simultaneously run for 50 million generations with sampling every 1000 generations. The first 25% of trees were removed as the "burn-in" stage followed by calculations of Bayesian posterior probabilities and the 50% majority-rule consensus of the post burn-in trees sampled at stationarity. Finally, genetic distance between species with uncorrected *p*-distance model on the 16S gene was estimated using MEGA.

2.3 Morphological analyses Twelve adult specimens of the

undescribed species and 13 adult specimens of *L. oshanensis* were measured (Table S1). Measurements were made with a dial caliper to the nearest 0.1 mm. The terminology and methods followed Fei *et al.* (2009), Ohler *et al.* (2011) and Rowley *et al.* (2016). Twenty-four morphometric characters were measured for adults: diameter of the exposed portion of the eyeball (EYE); maximum diameter of femoral gland (FEM); thigh length (FL), from middle cloaca to out edge of knee; forearm length (FLL), from elbow to base of outer palmar tubercle; largest forearm width (FLW); foot length (FOL), from base of inner metatarsal tubercle to tip of fourth toe; distance between middle of femoral gland and outer edge of knee (FTN); hand length, from base of outer palmar tubercle to tip of third finger (HAL); head length (HDL), measured at ventral view, the distance between the tip of snout to the line connecting posterior end of jaws; head width (HDW) at the commissure of the jaws; maximum diameter of humeral gland (HUM); internarial distance (IN); interorbital distance (IOD); distance from anterior edge of nostril to tip of snout (NS); maximum diameter of pectoral gland (PEC); distance from anterior corner of eye to nostril (SL); snout length, from tip of snout to the anterior corner of eye (SNT); snout-vent length (SVL); length of tarsus and foot (TFOL), from base of tarsus to tip of fourth toe; tibia length (TL); largest tibia width (TW); horizontal diameter of tympanum (TYD); distance between anterior margin of tympanum and posterior corner of eye (TYE); maximum width of upper eyelid (UEW).

Nine tadpole specimens of the undescribed species and eleven tadpole specimens of *L. oshanensis* were measured (Table S2). Description of lateral line system of tadpoles follows Lannoo (1987). Seventeen morphometric characters were measured for tadpoles: maximum body height (BH); body length, from tip of snout to conjunction of body and tail (BL); maximum body width (BW); maximum diameter of eye (ED); internarial distance (IND); keratodont row formula (KRF); maximum height of lower tail fin (LF); distance between nostril and eye (NE); oral disc width (ODW); interpupilar distance (PP); rostro-narial distance (RN); snout length, from tip of snout to the anterior corner of eye (SN); distance from tip of snout to opening of spiracle (SS); distance from snout to beginning of upper tail fin (SU); tail length (TAL); maximum tail muscle height (TMH); maximum tail muscle width (TMW); maximum height of upper tail fin (UF).

To reduce the impact of allometry, the correct value from the ratio of each character to SVL was calculated and then was log-transformed for the following morphometric analyses. Mann-Whitney *U* tests were conducted to test the significance of differences on morphometric characters between the undescribed species and *L. oshanensis*. The significance level was set at 0.05.

The undescribed species was also compared with all other congeners of *Leptobrachella* based on morphological characters. Comparative morphological data were obtained from literatures (Table 2).

2.4 Skull scanning Four adult specimens of *L. oshanensis* including two females (CIBEMS20190421SSG1-8 and CIBEMS20190421SSG1-10) and two males (CIBEMS20190421SSG1-11 and CIBEMS20190422SSG3-1) and four specimens of the undescribed species including two females (CIBEM1845 and CIBEMLGL19052104) and two males (CIBEMS20190422HLJ1-6 and CIBEMS20190422HLJ2-1) were scanned. Specimens were scanned along the coronal axis at an image resolution of 1024 × 1024 pixels in the high-resolution X-ray scanner (Quantum GX micro-CT Imaging System, PerkinElmer®). Segmentation and three-dimensional reconstruction of the CT images were made using VG57 Studio Max 2.2 (Volume Graphics, Heidelberg, Germany). Terminology of skull description follows Fei and Yei (2016).

2.5 Bioacoustics Advertisement calls of the undescribed species and *L. oshanensis* were recorded at a distance between 0.5–1.0 m by using a Philip VTR6900 digital voice recorder with a build-in microphone at sampling rate 96 kHz, bite rate 3072 kbps. All calls were recorded at temperature between 15 °C and 22 °C in April 2019. Calls were analyzed using Raven Pro© v.1.5 software (Bioacoustics Research Program, 2013) (window size 256 points, fast-Fourier transform, Hanning windows). Sonograms and spectrograms were presented in figures by Praat (Boersma *et al.*, 2001). Terminology of advertisement call analyses and description followed Köhler *et al.* (2017) and Wang *et al.* (2019). Call duration, dominant frequency, inter-call interval and note rise time were measured. Other call measurements as were taken as follows: the number pulses for the first note in a call (Note Pulses 1); the number pulses for the second note in a call (Note Pulses 2); the number pulses for the third note in a call (Note Pulses 3); the number pulses for the fourth note in a call (Note Pulses 4); the interval between the first note and the second note in a call (Note Interval 1); the interval between the second note and the third note in a call (Note Interval 2); the interval between the third note and the fourth note in a call (Note intervals 3); the frequency of first harmonic in a call (Harmonic 1); the frequency of second harmonic in a call (Harmonic 2); the frequency of third harmonic in a call (Harmonic 3).

Mann-Whitney *U* tests were conducted to test the significance of differences on call characters between the undescribed species and *L. oshanensis*. The significance level was set at 0.05.

3. Results

Molecular phylogenetic analyses Phylogenetic analyses were

Table 2 References for morphological characters for congeners of the genus *Leptobrachella*.

No.	*Leptobrachella* species	Literature obtained
1	*L. aerea* (Rowley, Stuart, Richards, Phimmachak and Sivongxay, 2010)	Rowley *et al.*, 2010a
2	*L. alpina* (Fei, Ye and Li, 1990)	Fei *et al.*, 1990
3	*L. applebyi* (Rowley and Cao, 2009)	Rowley and Cao, 2009
4	*L. arayai* (Matsui, 1997)	Matsui, 1997
5	*L. ardens* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen and Ziegler, 2016)	Rowley *et al.* 2016
6	*L. baluensis* (Smith, 1931)	Dring, 1983; Eto *et al.*, 2016, 2018
7	*L. bidoupensis* (Rowley, Le, Tran and Hoang, 2011)	Rowley *et al.*, 2011
8	*L. bijie* (Wang, Li, Li, Chen and Wang, 2019)	Wang *et al.*, 2019
9	*L. bondangensis* (Eto, Matsui, Hamidy, Munir and Iskandar, 2018)	Eto *et al.*, 2018
10	*L. botsfordi* (Rowley, Dau and Nguyen, 2013)	Rowley *et al.*, 2013
11	*L. bourreti* (Dubois, 1983)	Ohler *et al.*, 2011
12	*L. brevicrus* (Dring, 1983)	Dring, 1983; Eto *et al.*, 2015
13	*L. chishuiensis* Li, Liu, Wei and Wang, 2020	Li *et al.*, 2020
14	*L. crocea* (Rowley, Hoang, Le, Dau and Cao, 2010)	Rowley *et al.*, 2010b
15	*L. dringi* (Dubois, 1987)	Inger *et al.*, 1995; Matsui and Dehling, 2013
16	*L. eos* (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler and Dubois, 2011)	Ohler *et al.*, 2011
17	*L. feii* (Chen, Yuan, and Che, 2020)	Chen *et al.*, 2020
18	*L. firthi* (Rowley, Hoang, Dau, Le and Cao, 2012)	Rowley *et al.*, 2012
19	*L. flaviglandulosa* (Chen, Yuan and Che, 2020)	Chen *et al.*, 2020
20	*L. fritinniens* (Dehling and Matsui, 2013)	Dehling and Matsui, 2013
21	*L. fuliginosa* (Matsui, 2006)	Matsui, 2006
22	*L. fusca* (Eto, Matsui, Hamidy, Munir and Iskandar, 2018)	Eto *et al.*, 2018
23	*L. gracilis* (Günther, 1872)	Günther, 1872; Dehling, 2012a
24	*L. hamidi* (Matsui, 1997)	Matsui, 1997
25	*L. heteropus* (Boulenger, 1900)	Boulenger, 1900
26	*L. isos* (Rowley, Stuart, Neang, Hoang, Dau, Nguyen and Emmett, 2015)	Rowley *et al.*, 2015
27	*L. itiokai* Eto, Matsui and Nishikawa, 2016	Eto *et al.*, 2016
28	*L. juliandringi* Eto, Matsui and Nishikawa, 2015	Eto *et al.*, 2015
29	*L. kajangensis* (Grismer, Grismer and Youmans, 2004)	Grismer *et al.*, 2004
30	*L. kalonensis* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen and Ziegler, 2016)	Rowley *et al.*, 2016
31	*L. kecil* (Matsui, Belabut, Ahmad and Yong, 2009)	Matsui *et al.*, 2009
32	*L. khasiorum* (Das, Tron, Rangad and Hooroo, 2010)	Das *et al.*, 2010
33	*L. lateralis* (Anderson, 1871)	Anderson, 1871; Humtsoe *et al.*, 2008
34	*L. laui* (Sung, Yang and Wang, 2014)	Sung *et al.*, 2014
35	*L. liui* (Fei and Ye, 1990)	Fei *et al.*, 2009; Sung *et al.*, 2014
36	*L. macrops* (Duong, Do, Ngo, Nguyen and Poyarkov, 2018)	Duong *et al.*, 2018
37	*L. maculosa* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen and Ziegler, 2016)	Rowley *et al.*, 2016
38	*L. mangshanensis* (Hou, Zhang, Hu, Li, Shi, Chen, Mo and Wang, 2018)	Hou *et al.*, 2018
39	*L. maoershanensis* (Yuan, Sun, Chen, Rowley and Che, 2017)	Yuan *et al.*, 2017
40	*L. marmorata* (Matsui, Zainudin and Nishikawa, 2014)	Matsui *et al.*, 2014a
41	*L. maura* (Inger, Lakim, Biun and Yambun, 1997)	Inger *et al.*, 1997
42	*L. melanoleuca* (Matsui, 2006)	Matsui, 2006
43	*L. melica* (Rowley, Stuart, Neang and Emmett, 2010)	Rowley *et al.*, 2010c
44	*L. minima* (Taylor, 1962)	Taylor, 1962; Ohler *et al.*, 2011
45	*L. mjobergi* (Smith, 1925)	Eto *et al.*, 2015, 2018
46	*L. nahangensis* (Lathrop, Murphy, Orlov and Ho, 1998)	Lathrop *et al.*, 1998
47	*L. namdongensis* (Hoang, Nguyen, Luu, Nguyen and Jiang, 2019)	Hoang *et al.*, 2019
48	*L. natunae* (Günther, 1895)	Günther, 1895
49	*L. neangi* (Stuart and Rowley, 2020)	Stuart and Rowley, 2020
50	*L. niveimontis* (Chen, Yuan and Che, 2020)	Chen *et al.*, 2020
51	*L. nokrekensis* (Mathew and Sen, 2010)	Mathew and Sen, 2010
52	*L. nyx* (Ohler, Wollenberg, Grosjean, Hendrix, Vences, Ziegler and Dubois, 2011)	Ohler *et al.*, 2011
53	*L. oshanensis* (Liu, 1950)	Liu 1950, 1961; this paper
54	*L. pallida* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen and Ziegler, 2016)	Rowley *et al.*, 2016
55	*L. palmata* Inger and Stuebing, 1992	Inger and Stuebing, 1992
56	*L. parva* Dring, 1983	Dring, 1983
57	*L. pelodytoides* (Boulenger, 1893)	Boulenger, 1893; Ohler *et al.*, 2011
58	*L. petrops* (Rowley, Dau, Hoang, Le, Cutajar and Nguyen, 2017)	Rowley *et al.*, 2017a
59	*L. picta* (Malkmus, 1992)	Malkmus, 1992
60	*L. platycephala* (Dehling, 2012)	Dehling, 2012b
61	*L. pluvialis* (Ohler, Marquis, Swan and Grosjean, 2000)	Ohler *et al.*, 2000, 2011
62	*L. puhoatensis* (Rowley, Dau and Cao, 2017)	Rowley *et al.*, 2017b
63	*L. purpuraventra* Wang, Li, Li, Chen and Wang, 2019	Wang *et al.*, 2019
64	*L. purpurus* (Yang, Zeng and Wang, 2018)	Yang *et al.*, 2018
65	*L. pyrrhops* (Poyarkov, Rowley, Gogoleva, Vassilieva, Galoyan and Orlov, 2015)	Poyarkov *et al.*, 2015
66	*L. rowleyae* (Nguyen, Poyarkov, Le, Vo, Ninh, Duong, Murphy and Sang, 2018)	Nguyen *et al.*, 2018
67	*L. sabahmontana* (Matsui, Nishikawa and Yambun, 2014)	Matsui *et al.*, 2014b
68	*L. serasanae* Dring, 1983	Dring, 1983
69	*L. shangsiensis* Chen, Liao, Zhou and Mo, 2019	Chen *et al.*, 2019
70	*L. sola* (Matsui, 2006)	Matsui, 2006
71	*L. suiyangensis* (Luo, Xiao, Gao and Zhou, 2020)	Luo *et al.*, 2020
72	*L. sungi* (Lathrop, Murphy, Orlov and Ho, 1998)	Lathrop *et al.*, 1998
73	*L. tadungensis* (Rowley, Tran, Le, Dau, Peloso, Nguyen, Hoang, Nguyen and Ziegler, 2016)	Rowley *et al.*, 2016
74	*L. tamdil* (Sengupta, Sailo, Lalremsanga, Das and Das, 2010)	Sengupta *et al.*, 2010
75	*L. tengchongensis* (Yang, Wang, Chen and Rao, 2016)	Yang *et al.*, 2016
76	*L. tuberosa* (Inger, Orlov and Darevsky, 1999)	Inger *et al.*, 1999
77	*L. ventripunctata* (Fei, Ye and Li, 1990)	Fei *et al.*, 2009
78	*L. wuhuangmontis* Wang, Yang and Wang, 2018	Wang *et al.*, 2018
79	*L. wulingensis* Qian, Xiao, Cao, Xiao, and Yang, 2020	Qian *et al.*, 2020
80	*L. yingjiangensis* (Yang, Zeng and Wang, 2018)	Yang *et al.*, 2018
81	*L. yunkaiensis* Wang, Li, Lyu and Wang, 2018	Wang *et al.*, 2018
82	*L. zhangyapingi* (Jiang, Yan, Suwannapoom, Chomdej and Che, 2013)	Jiang *et al.*, 2013

based on a 563 bp dataset for 16S gene and a 1035 bp dataset for nuclear gene RAG1. BI and ML analyses resulted in essentially identical topologies on 16S gene (Figure 2A), as well on RAG1 gene (Figure 2B). In all trees, all samples of the undescribed species were strongly clustered into one clade deeply nested into the *Leptobrachella* clade. In 16S gene trees, the undescribed species occupied an independent clade with unresolved relationships with nine closely-related species, i.e., *L. oshanensis*, *L. alpina*, *L. purpurus*, *L. bourreti*, *L. eos*, *L. bijie*, *L. purpuraventra*, *L. chishuiensis*, and *L. suiyangensis*. In RAG1 gene trees, the undescribed species

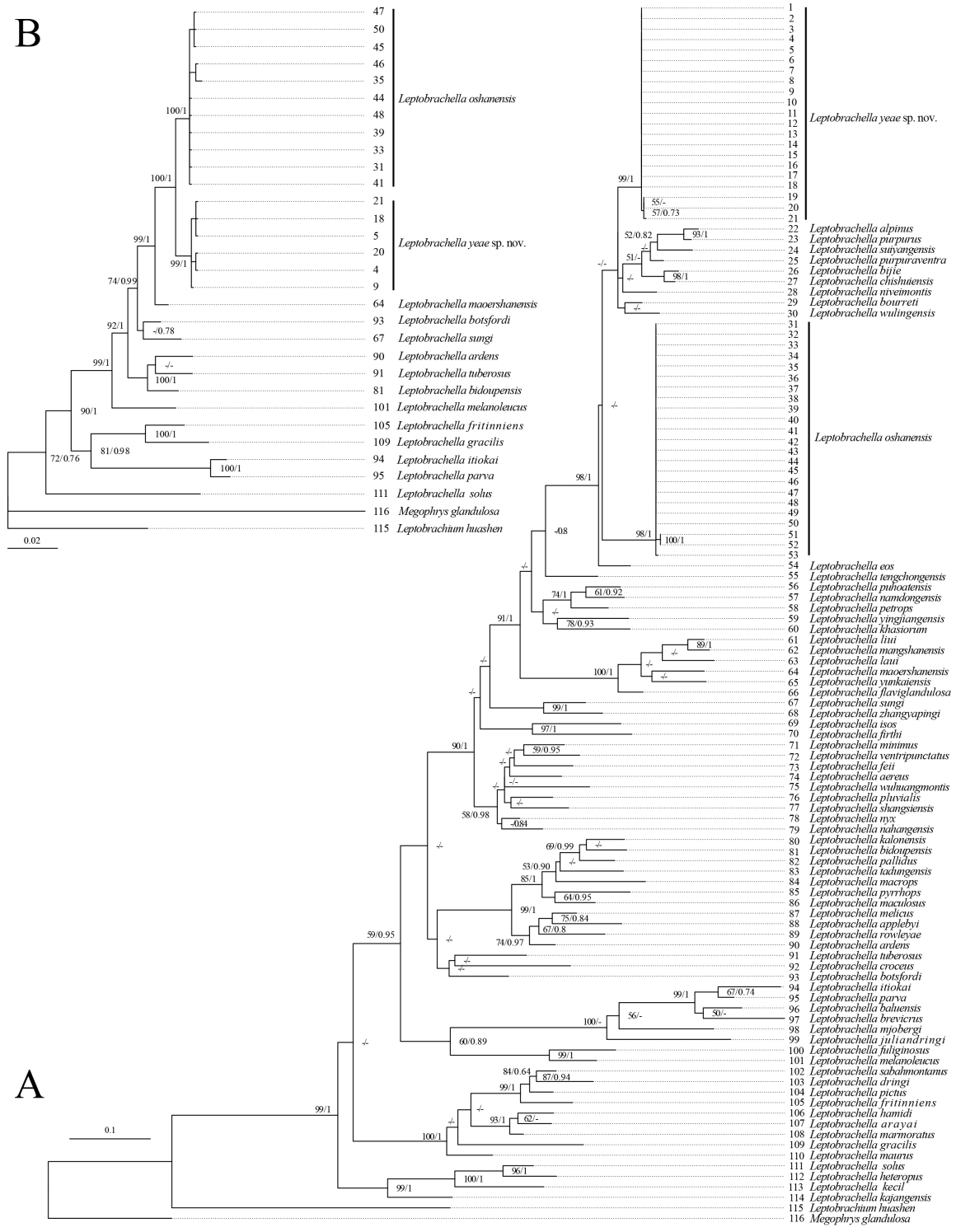

Figure 2 Phylogenetic trees respectively based on the mitochondrial 16S gene and nuclear RAG-1 gene sequences. A Maximum Likelihood (ML) tree based on the mitochondrial DNA. B ML tree based on the nuclear DNA. ML bootstrap support/Bayesian posterior probability was denoted beside node. Samples 1–116 refer to Table 1.

occupied a clade which was separated from and sister to the *L. oshanensis* clade in absence of other above related species. Genetic distances on 16S gene between all samples of the undescribed species were 0–0.4%. The undescribed species is closest to *L. bourreti* on genetic distance (3.7%), being higher than or at the same level with many pairs of substantial species, such as *L. bijie vs. L. chishuiensis* (1.8%), *L. eos vs. L. purpura* (3.4%), *L. purpuraventra vs. L. chishuiensis* (2.8%), and *L. wulingensis vs. L. bourreti* (2.8%; Table S3).

Morphological analyses. Mann-Whitney *U* tests between the undescribed species and *L. oshanensis* demonstrate non-significant differences in 23 measurements, and only the diameter of humeral gland of the undescribed species is significantly different from that of *L. oshanensis* ($P < 0.05$; Table 3). The undescribed species is different from *L. oshanensis* and its congeners on several morphological characters, such as adult skin texture, dorsal coloration, and dark gray patch on posterior thigh (Table 4). Detailed comparisons see the following description section of the undescribed species.

Skull. The nasal of male *L. oshanensis* is completely in contact with sphenethmoid (Figure 3A), but the nasal of the male undescribed species entirely or partially separated from sphenethmoid (Figure 3B). Details see the following description

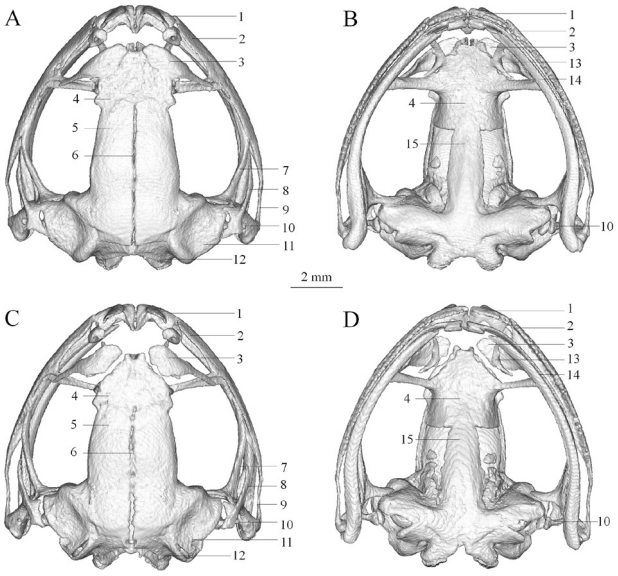

Figure 3 Skulls of *Leptobrachella yeae* sp. nov. and *L. oshanensis*. A, B dorsal and ventral views of adult male CIBEMS20190422SSG3-1 of *L. oshanensis*. C, D dorsal and ventral views of adult male holotype CIBEMS20190422HLJ2-1 of *Leptobrachella yeae* sp. nov. 1, premaxillary; 2, maxillary; 3, nasal; 4, sphenethmoid; 5, frontoparietal; 6, sagittal suture; 7, pterygoid; 8, squamosal; 9, quadratojugal; 10, columella auris; 11, prootic; 12, exoccipital; 13, vomer; 14, mandible; 15, anterior process of parasphenoid.

Table 3 Morphometric comparisons between *Leptobrachella yeae* sp. nov. and *L. oshanensis*. Units in mm. *P*-value was from Mann-Whitney *U* test for male. See abbreviations for morphometric characters in Materials and methods section.

Character	*Leptobrachella yeae* sp. nov.			*L. oshanensis*			*P*-value
	Male (n = 10)		Female (n = 2)	Male (n = 11)		Female (n = 2)	
	Range	Mean ± SD	Range	Range	Mean ± SD	Range	
SVL	25.8–31.2	28.7 ± 1.5	33.66–34.06	26.5–30.5	28.7 ± 1.4	28.8–32.6	0.973
HDL/SVL	0.334–0.394	0.362 ± 0.019	0.325–0.356	0.350–0.392	0.367 ± 0.016	0.337–0.349	0.705
HDW/SVL	0.320–0.386	0.344 ± 0.019	0.308–0.335	0.316–0.369	0.345 ± 0.014	0.327–0.327	0.756
SNT/SVL	0.129–0.160	0.144 ± 0.010	0.132–0.133	0.127–0.148	0.140 ± 0.007	0.137–0.148	0.282
EYE/SVL	0.110–0.129	0.121 ± 0.006	0.107–0.122	0.111–0.135	0.125 ± 0.007	0.120–0.122	0.197
IOD/SVL	0.103–0.119	0.111 ± 0.005	0.108–0.115	0.098–0.118	0.108 ± 0.005	0.103–0.115	0.251
IN/SVL	0.095–0.118	0.107 ± 0.006	0.097–0.099	0.089–0.117	0.101 ± 0.008	0.093–0.096	0.114
UEW/SVL	0.084–0.099	0.091 ± 0.005	0.080–0.080	0.083–0.093	0.090 ± 0.003	0.089–0.094	0.314
SL/SVL	0.069–0.082	0.075 ± 0.004	0.069–0.085	0.064–0.092	0.079 ± 0.008	0.071–0.084	0.099
NS/SVL	0.057–0.067	0.063 ± 0.003	0.057–0.062	0.051–0.067	0.060 ± 0.005	0.056–0.057	0.197
TMP/SVL	0.059–0.071	0.064 ± 0.003	0.058–0.061	0.054–0.075	0.066 ± 0.007	0.067–0.069	0.468
TYE/SVL	0.034–0.047	0.040 ± 0.004	0.035–0.042	0.034–0.057	0.046 ± 0.006	0.039–0.041	0.061
HAL/SVL	0.227–0.266	0.247 ± 0.012	0.234–0.241	0.235–0.269	0.247 ± 0.010	0.234–0.241	0.863
FLL/SVL	0.215–0.249	0.232 ± 0.011	0.218–0.223	0.214–0.246	0.235 ± 0.010	0.233–0.246	0.468
FLW/SVL	0.068–0.082	0.075 ± 0.004	0.059–0.06	0.066–0.086	0.075 ± 0.006	0.054–0.064	1.000
FL/SVL	0.437–0.476	0.457 ± 0.014	0.425–0.44	0.424–0.481	0.460 ± 0.016	0.424–0.447	0.705
TL/SVL	0.440–0.512	0.481 ± 0.021	0.443–0.452	0.445–0.495	0.475 ± 0.014	0.449–0.459	0.387
TW/SVL	0.110–0.129	0.120 ± 0.006	0.104–0.115	0.110–0.126	0.120 ± 0.005	0.098–0.102	0.973
FOL/SVL	0.403–0.497	0.447 ± 0.026	0.420–0.432	0.421–0.490	0.441 ± 0.019	0.408–0.414	0.314
TFOL/SVL	0.646–0.766	0.704 ± 0.033	0.673–0.688	0.686–0.722	0.70 ± 0.013	0.660–0.688	0.654
PEC/SVL	0.034–0.056	0.044 ± 0.008	0.035–0.035	0.033–0.050	0.042 ± 0.014	0.013–0.037	0.529
FEM/SVL	0.014–0.029	0.023 ± 0.004	0.028–0.035	0.020–0.041	0.027 ± 0.007	0.015–0.023	0.426
HUM/SVL	0.008–0.029	0.018 ± 0.007	0.025–0.026	0.015–0.035	0.025 ± 0.007	0.019–0.032	**0.036**
FTN/SVL	0.172–0.211	0.193 ± 0.012	0.187–0.198	0.180–0.217	0.197 ± 0.012	0.196–0.206	0.605

Table 4 Morphological differences between *Leptobrachella yeae* sp. nov. and its congeners occurring north of the Isthmus of Kra.

Species	Male SVL (mm)	Black spots on flanks	Toes webbing	Fringes on toes	Ventral coloration	Dorsal skin texture
Leptobrachella yeae sp. nov.	25.8–32.6	Yes	Rudimentary	Narrow	Cream white with small brown specking on sides and upper abdomen	Relatively smooth with tiny granules
L. aerea	25.1–28.9	No	Rudimentary	Wide	Near immaculate creamy white, brown specking on margins	Finely tuberculate
L. alpina	24.0–26.4	Yes	Rudimentary	Wide in males	Creamy-white with dark spots	Relatively smooth, some with small warts
L. applebyi	19.6–22.3	Yes	Rudimentary	No	Reddish brown with white speckling	Smooth
L. ardens	21.3–24.7	Yes	No	No	Reddish brown with white speckling	Smooth-finely shagreened
L. bidoupensis	18.5–25.4	Yes	Rudimentary	Weak	Reddish brown with white speckling	Smooth
L. bijie	29.0–30.4	Yes	Rudimentary	Narrow	White with distinct nebulous greyish speckling on chest and ventrolateral flanks	Shagreened and granular
L. botsfordi	29.1–32.6	No	Rudimentary	Narrow	Reddish brown with white speckling	Shagreened
L. bourreti	28.0–36.2	Yes	Rudimentary	Weak	Creamy white	Relatively smooth, some with small warts
L. chishuiensis	30.8–33.4	Yes	Rudimentary	Narrow	White with distinct nebulous greyish speckling on chest and ventrolateral flanks	Shagreened and granular
L. crocea	22.2–27.3	No	Rudimentary	No	Bright orange	Highly tuberculate
L. eos	33.1–34.7	No	Rudimentary	Wide	Creamy white	Shagreened
L. feii	21.5–22.8	Yes	Rudimentary	Narrow	Creamy white with black blotches	Shagreened with small tubercles and ridge
L. firthi	26.4–29.2	No	Rudimentary	Wide in males	Creamy white	Shagreened with fine tubercles
L. flaviglandulosa	23.0–27.0	Yes	Poorly developed	Narrow	Whitish, black speckling on margins	Shagreened with yellowish brown tubercles
L. fuliginosa	28.2–30.0	Yes	Rudimentary	Weak	White with brown dusting	Nearly smooth, few tubercles
L. isos	23.7–27.9	No	Rudimentary	Wide in males	Creamy white with white dusting on margins	Mostly smooth, females more tuberculate
L. kalonensis	25.8–30.6	Yes	No	No	Pale, speckled brown	Smooth
L. khasiorum	24.5–27.3	Yes	Rudimentary	Wide	Creamy white	Isolated, scattered tubercles
L. lateralis	26.9–28.3	Yes	Rudimentary	No	Creamy white	Roughly granular
L. laui	24.8–26.7	Yes	Rudimentary	Wide	Creamy white with dark brown dusting on margins	Round granular tubercles
L. liui	23.0-28.7	Yes	Rudimentary	Wide	Creamy white with dark brown spots on chest and margins	Round granular tubercles with glandular folds
L. macrops	28.0–29.3	Yes	Rudimentary	No	Greyish-violet with white speckling	Roughly granular with larger tubercles
L. maculosa	24.2–26.6	Yes	No	No	Brown, less white speckling	Mostly smooth
L. mangshanensis	22.22–27.76	Yes	Rudimentary	Weak	White speckles on throat and belly	Nearly smooth
L. maoershanensis	25.2–30.4	Yes	Rudimentary	Narrow	Creamy white chest and belly with irregular black spots	Longitudinal folds
L. melica	19.5–22.7	Yes	Rudimentary	No	Reddish brown with white speckling	Smooth
L. minima	25.7–31.4	Yes	Rudimentary	No	Creamy white	Smooth with tubercles and glandular folds
L. nahangensis	40.8	Yes	Rudimentary	No	Creamy white with light specking on throat and chest	Smooth
L. namdongensis	30.9	Yes	Rudimentary	No	Creamy white with brown dusting on margins	Finely tuberculate
L. neangi	35.4–36.3 in two adult females	Yes	no	no	belly transparent, immaculate purplish gray	Dorsal skin with small, irregular bumps and ridges
L. niveimontis	22.5–23.6	Yes	Rudimentary	Narrow	Marbling with black speckling	Relatively smooth with small tubercles
L. nokrekensis	26.0–33.0	Yes	Rudimentary	unknown	Creamy white	Not smooth, with tubercles and longitudinal folds
L. nyx	26.7–32.6	Yes	Rudimentary	No	Creamy white with white with brown margins	Rounded tubercles
L. oshanensis	26.5–30.5	Yes	Rudimentary	No	Whitish with no markings or only small, light grey spots	Shagreened, with fine dense granules and glandular ridges
L. pallida	24.5–27.7	No	No	No	Reddish brown with white speckling	Tuberculate
L. pelodytoides	27.5–32.3	Yes	Wide	Narrow	Whitish	Small, smooth warts
L. petrops	23.6–27.6	No	No	Narrow	Immaculate creamy white	Highly tuberculate
L. pluvialis	21.3–22.3	Yes	Rudimentary	No	Dirty white with dark brown marbling	Smooth, flattened tubercles on flanks
L. puhoatensis	24.2–28.1	Yes	Rudimentary	Narrow	Reddish brown with white dusting	Longitudinal skin ridges
L. purpura	25.0–27.5	Yes	Rudimentary	Wide	Dull white with indistinct grey dusting	Shagreen with small tubercles
L. purpuraventra	27.3–29.8	Yes	Rudimentary	Narrow	Grey purple with distinct nebulous greyish speckling on chest and ventrolateral flanks	Shagreened and granular
L. pyrrhops	30.8–34.3	Yes	Rudimentary	No	Reddish brown with white speckling	Slightly shagreened
L. rowleyae	23.4–25.4	Yes	No	No	Pinkish milk-white to light brown chest and belly with numerous white speckles	Smooth with numerous tiny tubercles
L. shangsiensis	24.9–29.4	Yes	Rudimentary	Narrow	Milk-white with dense whitish speckling	Mostly smooth with numerous tiny tubercles
L. suiyangensis	28.7–29.7	Yes	Rudimentary	Weak	yellowish creamy-white with distinct or indistinct light brown speckling mixed with marble texture	Shagreened and scattered with fine, rounded granules and short longitudinal folds
L. sungi	48.3–52.7	No or small	Wide	Weak	White	Granular
L. tadungensis	23.3–28.2	Yes	No	No	Reddish brown with white speckling	Smooth
L. tamdil	32.3	Yes	Wide	Wide	White	Weakly tuberculate
L. tengchongensis	23.9–26.0	Yes	Rudimentary	Narrow	White with dark brown blotches	Shagreened with small tubercles
L. tuberosa	24.4–29.5	No	Rudimentary	No	White with small grey spots/streaks	Highly tuberculate
L. ventripunctata	25.5–28.0	Yes	Rudimentary	No	Chest and belly with dark brown spots	Longitudinal skin ridges
L. wuhuangmontis	25.6–30.0	Yes	Rudimentary	Narrow	Greyish white mixed by tiny white and black dots	Rough, scattered with dense conical tubercles
L. wulingensis	24.5–32.8	Small to moderate	Rudimentary	Narrow	Creamy white, with distinct or indistinct brown speckling at margins	Shagreened with sparse large warts, sometimes with longitudinal ridges
L. yingjiangensis	25.7–27.6	Yes	Rudimentary	Wide	Creamy white with dark brown flecks on chest and margins	Shagreened with small tubercles
L. yunkaiensis	25.9–29.3	Yes	Rudimentary	Wide	Belly pink with distinct or indistinct speckling	Shagreened with short skin ridges and raised warts
L. zhangyapingi	45.8–52.5	No	Rudimentary	Wide	Creamy-white with white brown margins	Mostly smooth with distinct tubercles

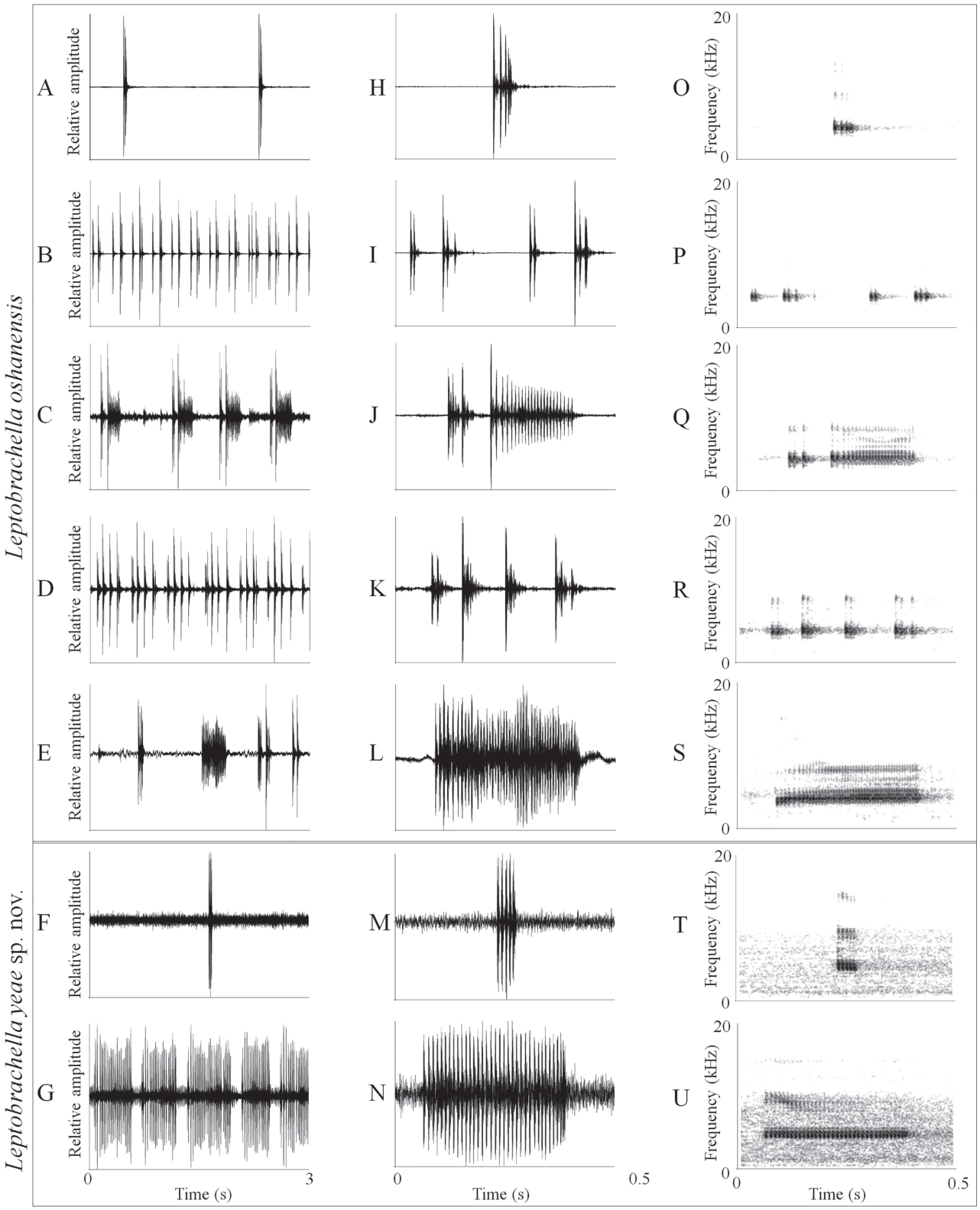

Figure 4 Visualization of advertisement calls of *Leptobrachella yeae* sp. nov. and *L. oshanensis*. A–E: five call types of *L. oshanensis*. F–G: two call types of *Leptobrachella yeae* sp. nov. A-G: waveform of relative amplitude over 3 seconds. H–N: waveform of relative amplitude over 0.5 seconds. O–U: spectrogram over 0.5 seconds.

sections of the undescribed species and *L. oshanensis*.

Bioacoustics. Calls of five males of *L. oshanensis* and six males of the undescribed species were measured (Table S4). The calls of *L. oshanensis* are complicated, consist of five types (Figure 4; Table 5; Table S4, type A to E). However, the calls of the undescribed species are much simpler, consist of two calls type. The two shared call types (types A and E) were different in dominant frequency, note rise time, frequency of harmonic 1 and 2, call duration and 1st Note Pulses between the two species (Table 5).

Taxonomy accounts

Leptobrachella oshanensis **(Liu, 1950)**

Figures 3C, 3D, 5–7, 8A, 9, 10A; Tables 1, 3, 4, 5, S1, S2, S4.

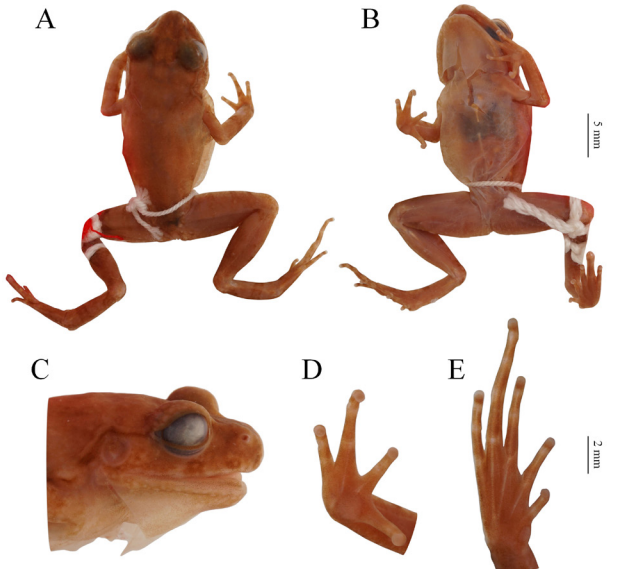

Figure 5 Photos for the holotype CIB24358 of *Leptobrachella oshanensis*. A: dorsal view. B: ventral view. C: lateral view of head. D: ventral view of hand. E: ventral view of foot.

Holotype: Figure 5. Adult male CIB24358 (collection number A1000, recorded as No. 1000), collected by Cheng-chao Liu on June 10, 1945. Type locality: Mt. Emei, Sichuan, China, recorded as "Mount Omei, Szechwan, 3500 feet altitude" in Liu (1950). Detailed location recorded as Da'esi according to original collection tag (spelled as "Taosze" in Liu, 1950).

Specimens examined. Holotype, adult male CIB24358(A1000), preserved in formalin. Ten sequenced adult males, two sequenced adult females and eleven tadpoles. Five adult males (CIBEMS20190421BGS5 to CIBEMS20190421BGS9), and one tadpole (CIBEMS20190421BGS1) were collected from a small mountain stream nearby Baoguosi, Mt. Emei (29.562957° N, 103.428375° E, ca. 702 m a.s.l) on April 21, 2019; two adult females (CIBEMS20190421SSG1-8 CIBEMS20190421SSG1-10), two adult males (CIBEMS20190421SSG1-9, CIBEMS20190421SSG1-11) and six tadpoles (CIBSC062, CIBSC063, CIBEMS20190422SSG1-1 to CIBEMS20190422SSG1-4; Figures 7, 8A) were collected from a stream nearby Da'esi in Mt. Emei (29.565086° N, 103.411304° E, 841 m a.s.l) on April 21, 2019; one adult male CIBEMS20190422SSG2-1 and two tadpoles CIBEMS20190422SSG3-2 and CIBSC064 were collected from the stream passing through Da'esi (29.563760° N, 103.409382° E, 827 m a.s.l) on April 22, 2019; one adult male CIBEMS20190422SSG3-1 (Figure 6) was from another small stream nearby Da'esi (29.564196° N, 103.410586° E, 824 m a.s.l) on April 22, 2019; one adult male (CIBEMS20190422SSG4-1) collected from a stream nearby Zhongfengsi (29.566393° N, 103.405375° E, 822 m a.s.l) on April 22, 2019; two tadpoles (CIBEMS20190422HLJ1-2 and CIBEMS20190422HLJ1-4) were collected from Heilongjiang (as "Heilungkiang" in Liu, 1950) (29.563762° N, 103.391465° E, 790 m a.s.l) on April 22, 2019. All topotype specimens collected by SC Shi.

Remarks. *Leptobrachella oshanensis* was described based on one male holotype and tadpoles from Heilongjiang ("Heilungkiang") and Da'esi ("Taosze") with numerous characters of the holotype missing. Fei and Ye (1992), Fei (1999) and Fei and Ye (2016) provided diagnoses, and Fei *et al.* (2009) provided measurements of sixteen characters of adults and ten characters of tadpoles based on specimens from Mt. Emei without voucher information. However, molecular analyses indicated that samples from Mt. Emei represent more than one species (Chen *et al.*, 2018; this study). Herein, updated description of holotype and variations, re-description of tadpole and measurements are based on sequenced specimens in the same lineage. Specimens assigned to *L. oshanensis* form a single lineage including

Table 5 Acoustic comparisons between *Leptobrachella yeae* sp. nov. and *L. oshanensis*. *P*-value was from Mann-Whitney *U* test.

Acoustic characters	Type E			Type A		
	Leptobrachella yeae sp. nov. Mean ± SD (*n* = 113)	*L. oshanensis* Mean ± SD (*n* = 43)	*P*-value	*Leptobrachella yeae* sp. nov. Mean ± SD (*n* = 6)	*L. oshanensis* Mean ± SD (*n* = 47)	*P*-value
Dominant Frequency (Hz)	4831.9 ± 155.8	4203.5 ± 172.7	0.000	4562.5 ± 214.1	4276.6 ± 139.8	0.010
Call Duration (ms)	544.5 ± 146.8	249.6 ± 61.7	0.000	70.3 ± 12.2	47.2 ± 13.6	0.001
Call Interval (ms)	353.7 ± 361.3	1521.6 ± 1581.8	0.000	2488 ± 1268.3	1524.1 ± 681	0.070
1st Note Pulses	34.0 ± 7.8	47.4 ± 7.0	0.000	7.2 ± 1.1	6.6 ± 2.1	0.288
Note Rise Time (ms)	62.4 ± 36.9	51.2 ± 67.9	0.000	29.7 ± 15.2	2.6 ± 0.7	0.000
Harmonic 1 (Hz)	9252 ± 554.6	8223.2 ± 387.2	0.000	9000 ± 530.3	8350 ± 496.2	0.006
Harmonic 2 (Hz)	14250 ± 265.2	12362.9 ± 374.8	0.000	14437.5 ± 187.5	12796.9 ± 427.1	0.004

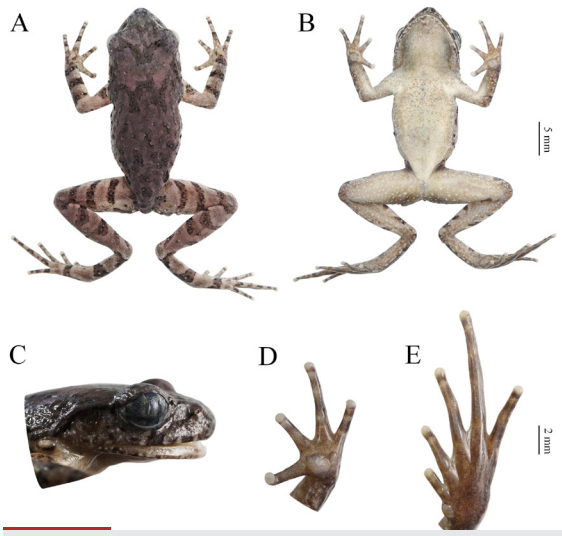

Figure 6 Photos for the adult male topotype specimen CIBEMS-20190422SSG3-1 of *Leptobrachella oshanensis*. A dorsal view. B ventral view. C lateral view of head. D ventral view of hand. E ventral view of foot.

specimens collected from the same small stream where the holotype was collected. Moreover, most adult individuals of these specimens resemble the holotype in morphology as Liu (1950) described: body reddish brown, fringes on toes very indistinct, posterior surface of thigh with blackish grey patches. Tadpoles were identified as *L. oshanensis* according to our molecular phylogenetic analyses.

Description of holotype. Figure 5. Measurements in mm. Body small (SVL 26.5); relatively slender. Head of medium size, longer than wide (HDL 10.2, HDW 9.1); snout bluntly rounded in profile and obtusely pointed in dorsal view, projecting slightly over lower jaw, slightly longer than horizontal diameter of eye (SNT 3.6, EYE 3.3); canthus rostralis distinct, loreal region concave, vertical; interorbital space flat, about as large (IOD 2.6) as internarial distance (IN 2.5), wider than upper eyelid (UEW 2.2); nostrils oval, closer to tip of snout (NS 1.5) as to eye (SL 2.1); tympanum (TMP 2.0) distinct, round, larger than half of horizontal eye diameter; tympanum-eye distance (TYE 1.5) three-fourths of tympanum diameter; tongue moderately broad, notched behind.

Forelimbs. Arms are weak, forearm moderate long (FLL 5.7), shorter than hand (HAL 6.7), not enlarged (FLW 1.8). Fingers long and thin, relative finger lengths: I < II < IV < III; tips of fingers slightly enlarged, rounded; nuptial pad absent; subarticular tubercles absent; inner palmar tubercle large, rounded, distinctly separated from outer palmar tubercle diameter more than twice of the latter; fingers without dermal fringe.

Hindlimbs. Slender, length 158% of body length, tibiotarsal articulation reaches the middle of eye; shank length equal to foot length, and subequal to thigh length, 3.7 times of its width (FL 11.9 TL 11.8, TW 3.2, FOL 11.9, TFOL 18.2); toes rudimentary webbed: I 2 – 3¼ II 2½ – 3¼ III 3 – 4¼IV4½ – 2¾ V, without lateral fringes (stated as extremely indistinct in Liu and Hu (1961)); subarticular tubercles absent; dermal ridges visible under second, third, fourth and fifth toes, continuously but narrower at articulations; inner metatarsal tubercle oval, short, outer metatarsal tubercle absent.

Skin. Skin on dorsum smooth, with few fine glandular ridges (cited from Liu 1950, ridges not visible when checked; possibly had fade away after seventy five years preservation in formalin); several small granules present on upper eye lids, dorsal arm, single granules present on transverse bands on dorsal thigh, several granules surround vent; ventral skin smooth; pectoral gland present on the dorso-basal part of the base of the arm (indistinguishable when checked, cited from Liu 1950); supratympanic fold distinct, from eye to above shoulder; femoral gland distinct (FEM 0.8), elongate, on posteroventral surface of thigh, closer to knee than to vent (FTN 5.2); humeral gland distinct, raised (HUM 0.8); pectoral glands invisible; ventrolateral glandular line present as separate glands in line (cited from Liu and Hu (1961), indistinguishable when checked).

Coloration in preservative. Figure 5. Dorsal parts of head and body uniformly brown; lateral head basically brown, upper lip lighter, with three deeper brown vertical short bars on each side; lower eyelid translucent, with a brown upper edge; tympanum lighter than skin around; skin beneath supratympanic fold deep brown; flanks lighter than dorsum; dorsal hands brown with two transverse bands on lower arm, and two or three bands on fingers; dorsal part of thigh, of shank and of foot light brown with darker brown crossbands; skin on ventral surface light brown, with deeper brown pigments on margin of mandible, and surround belly; femoral and humeral glands light colored.

Coloration in life. See description in Liu (1950) and Liu and Hu (1961).

Skull. (Figures 3A, B). Description based on sequenced adult male topotype CIBEMS20190422SSG3-1. Skull weakly ossified, feebly longer than wide, width 0.97 times of length; maxillary overlapping with quadratojugal; premaxillary and maxillary teeth moderately developed, no teeth on mandible; nasal process of premaxilla not protruding beyond skull, invisible from ventral view; nasal bones separated from each other, formed by an elongated base and sharp protruding, base completely connected with sphenethmoid; sphenethmoid rough, covered with pits on dorsal surface, relatively smooth on ventral surface, middle one sixth of front edge flat and free from nasal bones, protruding forward but not exceeding the nasal, a small bump present on lateral edges near frontoparietal where widest; frontoparietal divided by a small sagittal suture, anterior fontanelle absent; posterior frontoparietal slightly wider than anterior; posterior edge of exoccipitals posterior to the line

connecting conjunctions of quadratojugal and mandible; pterygoid moderate; anterior process of squamosal slender and sharp, tip closer to the junction of pterygoid and quadratojugal than its base, posterior process short and blunt; prootic large, fully connected with exoccipitals, partial separated from squamosal by small gaps; vomer small, crescent, without teeth and ridges, half in contact with sphenethmoid; parasphenoid large and strong, anterior process widest at its base; columella auris long, protruding beyond prootic from dorsal view.

Sexual dimorphism. Adult males with internal single subgular vocal sac, without nuptial pads on fingers. Spines on males' chest and belly while breeding absent. Lower arms not enlarged, linea musculina not visible on most individuals except on few (e.g. Figure 9 H). Breeding males with femoral adipose glands, a pair of macroglands attached to inner side of skin on posterior ventral surface of thigh, extending from cloaca and reaches femoral glands, consist of numerous dense yellowish white adipose granules, visible from ventral view of body when specimens alive (e.g. Figure 9 D F H). Femoral adipose glands are absent in females (Figure 9 B).

Advertisement call. Figures 4 A-E; Table S4. Calls recorded at temperature 19 to 22 ºC. Description based on five sequenced adults (Tables 1 and S4). Five call types were found, but a typical call series consists mainly of type B and/or type C. The first type (A) consists of repeated short notes; the second type (B) consists of two repeated short pulses separated from each other by a silent interval longer than its note interval; third type (C) consists of one short note and one following longer note; the fourth type (D) contains four notes, anterior three short, the last longer; the fifth (E) consists of long repeated notes. Type B and/or C consist main part a typical call series, while A, D and E are relatively fewer. Dominant frequency of all type of calls ranges from 4000.0 Hz to 4500.0 Hz. Dominant frequency of type B (4367.6 ± 179.2) Hz, type C (4383.9 ± 191.7) Hz, and type D (4481.3 ± 81.7) Hz slightly higher than that of type A (4276.6 ± 139.8) Hz and type E (4203.5 ± 172.7) Hz. Types A and E are more sparsely distributed in call series than other types, the inter-call intervals much longer (average 1040.3 ms to 1629.5 ms *vs.* 130.8 ms to 266.6 ms). Harmonic 1 and 2 are common, present on 99% and 70% of calls, harmonic 3 are much rare, only 1.7%. Amplitude of notes of call type A largest at first pulse, drastic reduce in following pulses; second note of type B possess amplitude larger than that of first note, and first pulses of two notes with largest amplitude; the second note of call type C with larger amplitude than the first note, amplitude reduce gradually on second note while radically on most first note; the second note of a typical D call type with largest amplitude, then gradually reduce in following notes; the amplitude of pulses of call type E are similar at beginning and end.

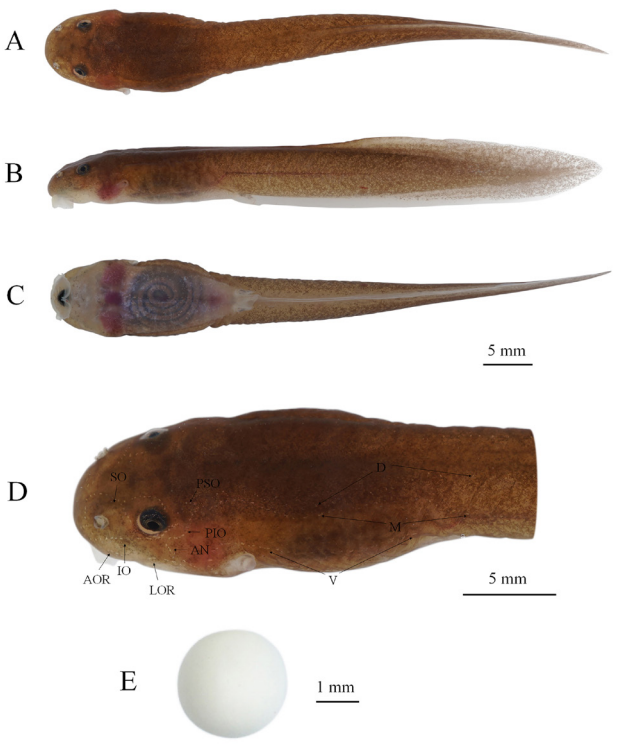

Figure 7 Photos for the tadpole CIBEMS20190422SSG1-1 in life and the egg of *Leptobrachella oshanensis*. A: dorsal view. B: lateral view. C: ventral view. D: dorsolateral view of head. E: unfertilized egg of female CIBEMS20190421SSG1-8. Abbreviations for characters: AN, angular; AOR, anterior oral; IO, infraorbital; SO, supraorbital; LOR, longitudinal oral; PIO, posterior infraorbital; PSO, posterior supraorbital; D, M, and V, dorsal, middle, and ventral body lines, respectively.

Tadpoles. Figures 7 A–D and 8 A. Measurements based on sequenced tadpoles see in Table 3 (in mm). Description base on sequenced tadpole CIBEMS20190422SSG1-1 in Gosner stage 34 (BL 18.6). Body elliptical elongate in dorsal view, widest at the level of heart, depressed in lateral view, BW 160% of BH, a pair of large lateral lymphatic sacs extending from spiracle to end of body; snout moderate, rounded, SN 22% BL; eyes moderate small, 7.8% of BL, slightly bulging on dorsolateral head; pineal ocellus and nasolacrymal ducts invisible; nostrils near oval, moderate large, rimed by three and four small lobes on left and right side, closer to pupil than tip of snout, RN 148% of NE; PP 115% of IND; spiracle short, tube like, oriented posterodorsally, SS 47% of BL, opening slightly closer to ventral surface than dorsal surface. Tail long and strong, tail musculature well developed, TAL 209% of BL, TWH 90% of BH, TMW 58% BW; upper fin absent in proximal third, then rise slowly, moderate shallow in following part, SU 129% of BL; lower fin convex, attached to anal tube, LF 64% of UF; anal tube short, moderately large, opening large, lateral, on right side and posterolaterally directed; glands on body invisible.

Lateral line system (Figure 7 D): Dorsal body line begins after eye with distance to eye about twice eye diameter, and

passes above the lateral sac, then stretching along base of upper fin, end at tip of tail; middle body line start after eye beneath and parallel to dorsal body line, slightly curves down on middle body, then stretches along longitudinal axis on tail before slowly joins the dorsal body line at about two fifth of distal tail; ventral body line curves half around the spiracle and stretches along body axis on middle lateral sac, end before constriction between body and tail; the angular line curves behind the eye and mostly transverse; anterior oral line not connected with longitudinal oral line, supraorbital and infraorbital line present, circling nostril and eye; an unnamed line connecting supraorbital line half separating regions around nostril and eye; posterior infraorbital and posterior supraorbital line present, the system is symmetrical on both sides of the tadpole. Lateral line organs dash-shaped, mostly longitudinally oriented except those of dorsal body line, the unnamed line separating regions around nostril and eye, the line connecting anterior infraorbital and anterior supraorbital line, angular and posterior infraorbital line.

Oral disc moderate (Figure 8 A), in shape of cup, transversely elongate, positioned and orient ventrally, not emarginated laterally, ODW 25% of BL and 55% of BW; lower labium divided, upper labium slightly concave in the middle; small papillae continuous on margin around oral disc, those on upper labium larger than those on lower labium; two submarginal papillae present laterally to keratodont rows of the lower labium and anteromedially to row P3; KRF I:3+3/2+2:I, keratodont rows short, A2 > A3 > A4 > A1; first row on upper labium shortest, the second slightly interrupted, other lower rows separated by upper beak; P1 > P2 > P3; P3 very short, one-third of P1; P2 about half of P1. Keratodonts scythe blade shaped. Jaw sheaths strong, coarsely serrated.

Coloration in life (Figures 7 A–D). Dorsal body and tail muscle uniformly rufous, colored by numerous spots formed by iridiophores; fins translucent covered by numerous rufous iridiophores, lower fin beneath the lower edge of proximal tail muscle completely transparent. Iris copper. Lateral body lighter than dorsal body, sacs not transparent. Ventral body transparent, covered with sparse copper iridiophores.

Coloration in preserve. Dorsal body and tail muscle pale brown; ventral part and fins greyish transparent.

Eggs. (Figure 7 E). Description based on unfertilized eggs laid by female CIBEMS20180421SSG1-8, a total of 163 eggs were counted. Eggs relatively large, diameter (2.5 ± 0.2) mm, range from 2.3 mm to 2.8 mm (n = 10), average diameter 7.7% of parent's SVL. Eggs uniformly cream white.

Variations. Measurements for adults see Table S1. The skin of holotype has lost some details after preserved in formalin for 75 years. Skin ridges not visible in recent examination but actually present according to Liu (1950); and dorsal skins were described as relatively smooth, scattered with fine granules, with six to eight light colored granules in rows from above shoulder to groin, basing on specimens collected from Mt. Emei according to Liu and Hu (1961). For fresh specimens collected in this study, dorsal skin of body, head, and limbs shagreened, dorsal body covered by fine dense granules, most with short or long granular skin ridges (Figure 9). Fringes on toes mostly absent, but one individual (CIBEMS20190421BGS7) with indistinct narrow fringes. Most outer palmar tubercle with diameter half of the inner, few about. Pectoral glands of fresh specimens mostly indistinct and flat; humeral gland distinct and raised; femoral glands flat. Ventrolateral glandular lines of fresh specimens present as separated spots, mostly indistinct. The linea musculina invisible in most adult males, weakly present on few.

The dorsal surface of most individuals uniformly reddish brown, one adult male (CIBEMS20190421BGS7; Figure 9 E,

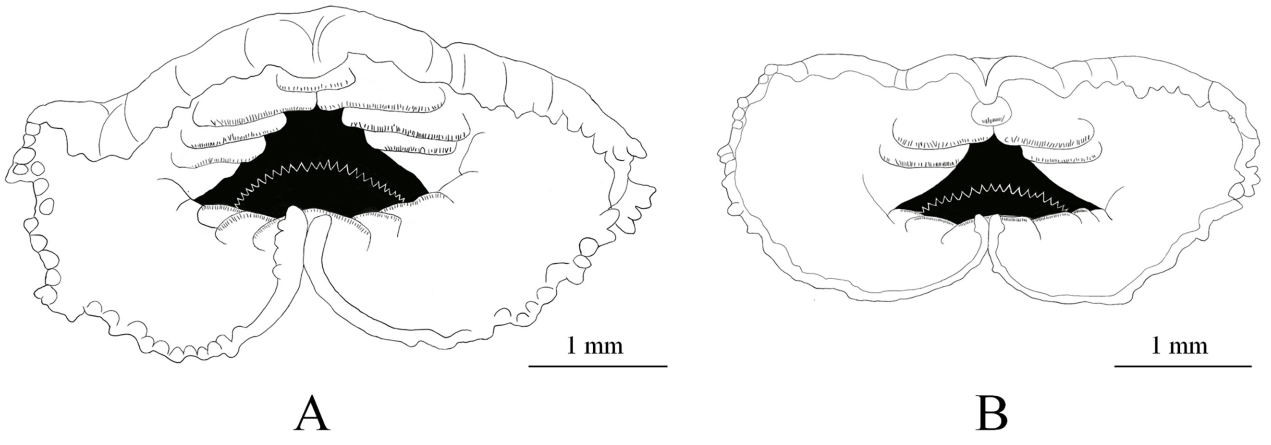

Figure 8 Simple drawings for the oral disc of tadpoles of *Leptobrachella oshanensis* and *Leptobrachella yeae* sp. nov. A tadpole CIBEMS20190422SSG1-1 of *L. oshanensis*, Gosner stage 34. B tadpole CIBEMS20190422HLJ1-1 of *L. yeae* sp. nov., Gosner stage 36. Lower keratodont rows were denoted as P1-P3, and upper keratodont rows were denoted as A1-A4.

Figure 9 Photos showing colour variation in topotypes of *Leptobrachella oshanensis* in life. A, B: dorsolateral and ventral views of adult female CIBEMS20190421SSG1-8, respectively. C, D: dorsolateral and ventral views of adult male CIBEMS20190422SSG4-1, respectively. E, F: dorsolateral and ventral views of adult male CIBEMS20190421BGS7, respectively. G: dorsolateral view of adult male CIBEMS20190421BGS7. H: ventral view of adult male CIBEMS20190422SSG2-1.

F) grey brown. All adult individuals with brown "V" shaped pattern on snout, a brown triangular pattern on head between upper eyelids, and a brown "W" shaped pattern on shoulder, irregular small patches or stripes surround warts or skin ridges present on lower dorsum. Dorsal limbs mostly reddish brown; dorsal upper arm and tibiotarsal articulation slightly lighter, but dorsal upper arm of CIBEMS20190421BGS7 yellowish grey; brownish cross bands present on dorsal lower arms, fingers, thighs, and foot. Upper lips with three brownish bands, present before nostril, on loreal, and below eye. Supratympanic fold with dark stripe on lower edge. Most part of tympanum deep brown. Flanks with several large dark patches. Ventral body light colored; throat pinkish with light smoky brown, margin brown with cream dots; chest and belly yellowish cream, with light brown specking on all chest, entire or lateral belly; ventral thigh pinkish, purplish, or faint white; a large greyish black patche present between two yellowish cream femoral glands on posterior surface of thigh; humeral glands buff; pectoral glands yellowish cream. Upper iris color gold when living, lower iris silver, both with deep brown dendritic strips. The linea musculina cream white when present.

Skull variation. A total of four sequenced specimens were scanned, two adult females CIBEMS20190421SSG1-8, CIBEMS20190421SSG1-10 and two adult males CIBEMS20190422SSG3-1, CIBEMS20190421SSG1-11. The four skulls generally similar. The nasal of female EMS20190421SSG1-8 and CIBEMS20190421SSG1-10 completely separated from sphenethmoid. And squamosal of the two females entirely separated from prootic. Vomer of the two females isolated from sphenethmoid. The sphenethmoid of male paratype CIBEMS20190422HLJ1-6 exceed nasal.

Variation of tadpoles' measurements see in Table S2. Lateral line system of other tadpoles similar with CIBEMS20190422SSG1-1, but one tadpole with angular line stretch into orbit instead of curving behind eye (CIBEMS20190421BGS1). Coloration on tadpoles at earlier stage lighter. Small irregular transparent dots on tail formed by absence of iridophores presents on fins of some tadpoles. KRF mostly I: 3+3/2+2: I, one in twelve I: 3+3/3+3: I (CIBEMS20190422SSG3-2 at Gosner stage 32).

Distribution and ecology. Since there many cryptic species (Chen *et al.*, 2018), the distribution range of *L. oshanensis* should be limited to southwestern edge of Sichuan Basin. This species was found calling on stream sides or under blocks steeped in stream under broad leaf forest (Figure 10 A) from April 21 to June 10 at elevation between 702 to 1067 m. Gravid female recorded on April 22 with eggs well developed. Five species of Megophryidae found to be sympatric with *L. oshanensis*: the undescribed species, *Megophrys omeimontis*, *M.* cf. *minor*, *Leptobrachium boringii*, *Oreolalax omeimontis*, and *O. popei*.

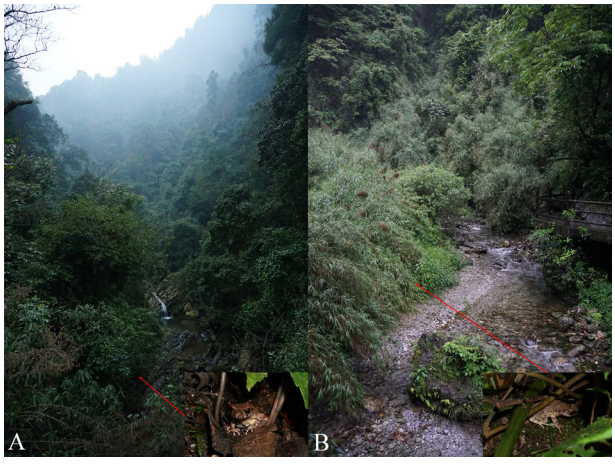

Figure 10 Habitats of *Leptobrachella oshanensis* and *Leptobrachella yeae* sp. nov. in Emei Mountain, Sichuan Province, China. A: adult male CIBEMS20190421BGS8 of *L. oshanensis* (insert) founded calling on a stream banks at Baoguosi in Emei Mountain. B: adult male EMS20190422HLJ1-7 of *L. yeae* sp. nov. (insert) founded calling on the ground nearby the Heilongjiang river in Emei Mountain.

***Leptobrachella yeae* sp. nov.**

Figures 3 B, 4 F, 4 G, 8 B, 11, 12, 13, 14; Tables 1, 3, 4, 5, S1, S2, and S4

Holotype. Figures 11, 12. CIBEMS20190422HLJ2-1, adult male, collected by SC Shi from Heilongjiang river, Emei Mountain, Leshan City, Sichuan Province (29.565906° N, 103.393002° E, 783 m a.s.l), China, calling under herbs at 22:56 on April 22, 2019.

Paratypes. Ten adult males and two adult females. Six adult males, collected from a small side stream of Heilongjiang river (29.563762° N, 103.391465° E, 790 m a.s.l) on May 5, 2018 (CIBEM1839 to CIBEM1841), and April 22, 2019 (CIBEMS20190422HLJ1-6 to CIBEMS20190422HLJ1-8) by SC Shi. One gravid female (CIBEM1845) and three adult males (CIBEM1842, CIBEM1844, CIBEM1849) collected from the small stream at Changshouqiao, near Yuxiansi (29.557010° N, 103.352900° E, 1806 m a.s.l.) on May 4, 2018 by SC Shi. One adult female (CIBEMLGL19052104) collected from a stream at Linggongli (29.583945° N, 103.294208° E, 1367 m a.s.l.) by YM Hou and WB Zhu on May 21, 2019.

Other specimens examined. Nine tadpoles. Seven (CIBEM1867, CIBSC066, and CIBSC068 to CIBSC072) from Changshouqiao on May 3 and 4, 2018, and two from Heilongjiang (CIBEMS20190422HLJ1-1, CIBEMS20190422HLJ1-3) on May 21, 2019, all tadpoles collected by SC Shi.

Diagnose. The new species is assigned to the genus *Leptobrachella* based on following characters: size small or moderate; fingertips rounded, inner palmar tubercle elevated not continuous to the thumb, much larger than outer palmar tubercle; macroglands present on body; vomerine teeth absent; tubercles on eyelids present; anterior tip of snout with whitish vertical bar (Dubois, 1983; Matsui, 1997, 2006; Lathrop *et al.*, 1998; Delorme *et al.*, 2006; Das *et al.*, 2010).

The new species differs from its congeners by a combination of following characters: body size moderate (25.8–32.6 mm in ten males; 33.7–34.1 mm in two females); distinct black spots present on flanks; toes rudimentary webbed, with narrow lateral fringes, dermal ridges under toes interrupted at articulations; dorsal body coloration vary (deep brown, orange brown, greyish brown, or yellowish brown) but not purple brown; ventral belly cream white with variable brown specking; skin on dorsum relatively smooth with fine tiny granules or short ridges; iris copper above, silver bellow; greyish black patches on posterior thigh absent or small; dense tiny conical spines on surface of chest absent in male during breeding season; nasals entirely or partially separated from sphenethmoid in male; dorsal surface of tadpoles semitransparent light brown, spots on tail absent, keratodont row formula I: 3+3(2+2)/2+2: I; calls simple, call series basically consist of repeated long calls, at

Figure 11 Photos for the holotype CIBEMS20190422HLJ2-1 of *Leptobrachella yeae* sp. nov. A: dorsal view. B: ventral view. C: lateral view of head. D: ventral view of hand. E: ventral view of foot.

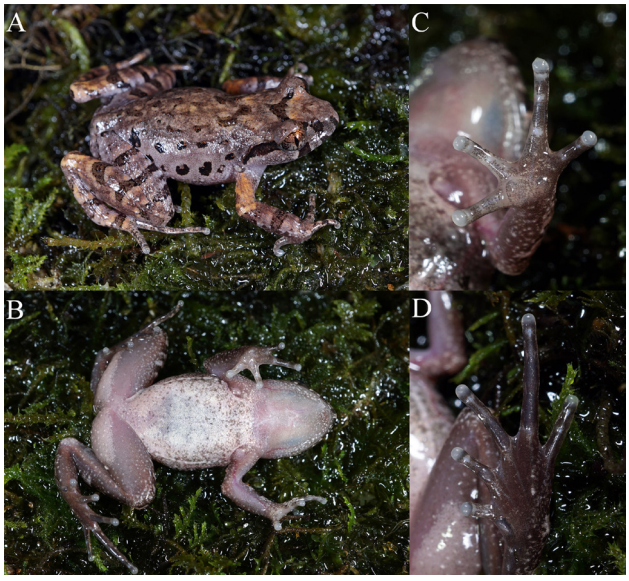

Figure 12 Photos for the holotype CIBEMS20190422HLJ2-1 of *Leptobrachella yeae* sp. nov. in life. A: dorsal view. B: ventral view. C: ventral view of hand. D: ventral view of foot.

dominant frequency (4831.9 ± 155.8) Hz and call duration (544.5 ± 146.8) ms.

Holotype description. Figures 11 and 12. Measurements in mm. Body size moderate (SVL 28.8), weight 2.0 g when living. Head longer than wide (HDL 9.8, HDW 9.2); snout bluntly rounded in profile and obtusely pointed in dorsal view, slightly projecting over lower jaw, longer than eye diameter (SNT 3.7, EYE 3.2); canthus rostralis distinct, loreal region concave, vertical; interorbital space (IOD 3.2) flat, slightly wider than internarial

distance (IN 3.0), distinctly larger than upper eyelid (UEW 2.4); nostrils oval, closer to tip of snout than eyes (NS 1.8, SL 2.2); tympanum distinct (TMP 1.9), rounded, larger than half of eye diameter, distance to eye about two thirds of its diameter (TYE 1.2); tongue moderately broad, notched behind.

Forelimbs. Weak, forearm moderate long (FLL 6.8), shorter than hand (HAL 7.3), not enlarged (FLW 1.8). Fingers moderate, relative finger lengths: I < II < IV < III; fingertips slightly dilated; nuptial pad absent; subarticular tubercles absent; inner palmar tubercle large, nearly rounded, outer palmer tubercle small, completely separated; fingers without lateral dermal fringe.

Hindlimbs. Relatively long, length 165% of body length; shank length about equal to foot length, subequal to thigh length, 4.0 times of its width (FL 13.2, TL 14.1, TW 3.5, FOL 13.1, TFOL 20.2); heels partially overlapped when thighs are positioned at right angles to the body and tibia-tarsal articulation reaches the middle eye when leg stretched; toes rudimentary webbed: I 2–3 II 2–3¼ III 2¾–4 IV 4¼–2½ V, with distinct narrow fringes; subarticular tubercles absent; dermal ridges under toes (except the first) distinct under toes and interrupted at articulations; inner metatarsal tubercle oval, short, outer metatarsal tubercle absent.

Skin. Dorsal body and head smooth, with tiny sparse granules, no glandular ridges; several small bump present on upper eye lids; dorsal arms and hindlimbs with tiny granules and bumps; lateral head smooth. Ventral skin smooth. Pectoral glands indistinct and flat (PEC 1.6); femoral glands slightly swollen (FEM 0.8), distinct on posterior thigh, closer to outer edge of knee than vent (FTN 6.0); humeral glands raised, distinct (HUM 0.8); ventrolateral line present as interrupted line from after axilla to near groin. Linea musculina invisible.

Coloration in preservation. Dorsal body and head grey brown, with a triangular dark brown marking between upper eyelids, and deep grey brown irregular patches on shoulder, patches surrounded by pale grey; lateral head grey, with three vertical dark brown bands before nostril, on loreal region, and below anterior part of eye; skins beneath supratympanic fold dark brown, including most part of tympanum and upper part of temporal; lower flanks grey, covered with five and eight large dark brown patches on left and right respectively, some patches with size about tympanum; dorsal limbs and digits light brown with deep brown cross bands except dorsal upper arms, bands on hindlimbs edged with pale grey; posterior thigh without greyish black color from ventral view, with a deep brown stripe from dorsal view; throat smoky light brownish yellow, with yellowish cream spots on margin; chest and belly yellowish cream, with light brown small specking, dense on chest and lateral belly; ventral thigh and anterior arms yellowish, ventral tibia and posterior arms deeper; ventral limbs scattered with tiny light yellow dots; pectoral, femoral, and humeral glands, ventrolateral line yellowish cream.

Coloration in life. Dorsal body and head yellowish brown, markings on head and dorsum medium brown; dorsal limbs basically yellowish brown, dorsal upper arms and tibiotarsal articulation yellow, cross bands light brown; lateral head and flanks greyish brown with dark patches; ventral surfaces light colored; throat and ventral arms pinkish with cream specking on margins; chest and belly cream white with light brown speckling, which dense on chest and lateral belly; ventral hindlimbs pinkish with sparse cream specking, no greyish dark patches on posterior thigh; ventrolateral line, femoral glans, pectoral glands cream, humeral glands greyish buff; upper iris copper, lower iris silver, both parts with several dendritic dark gaps.

Skull. Figure 3 C, D. Skull weakly ossified, slightly longer than wide, width 0.97 times of length; maxillary overlapping with quadratojugal; premaxillary and maxillary teeth moderately developed, no teeth on mandible; nasal process of premaxilla not protruding beyond skull, invisible from ventral view; nasal bones widely separated from each other, base entirely separated from sphenethmoid; sphenethmoid relatively smooth on ventral surface, middle one sixth of front edge flat and free from nasal bones, protruding forward but not exceeding the nasal, a small bump present on lateral edges near frontoparietal where widest; frontoparietal divided by a small sagittal suture, anterior fontanelle absent; posterior frontoparietal slightly wider than anterior; posterior edge of exoccipitals posterior to the line connecting conjunctions of quadratojugal and mandible; pterygoid moderate; anterior process of squamosal slender and sharp, tip closer to the junction of pterygoid and quadratojugal than its base, posterior process hardly present; prootic large, partial separated from exoccipitals by narrow gap, entirely separated from squamosal; vomer small, crescent, without teeth and ridges, entirely separated from sphenethmoid; parasphenoid large and strong, anterior process widest at its base; columella auris long, protruding beyond prootic from dorsal view.

Sexual dimorphism. Adult males with internal single subgular vocal sac, without nuptial pads on fingers. Spines on males' chest and belly while breeding absent. Lower arms not enlarged, linea musculina not visible on most individuals except on few (e.g., Figure 13 H). Breeding males with femoral adipose glands, extending from cloaca and reaches femoral glands, consist of numerous yellowish white adipose granules (e.g. Figures 12 B, 13 D, F, H). Femoral adipose glands absent in females (Figure 13 B).

Advertisement call. Figure 4 F, G. Call description based on the calls of the holotype, two paratypes and two unvouchered males. Calls contain two different type, repeated short call (type A) and repeated long call (type E). A typical call series consist of

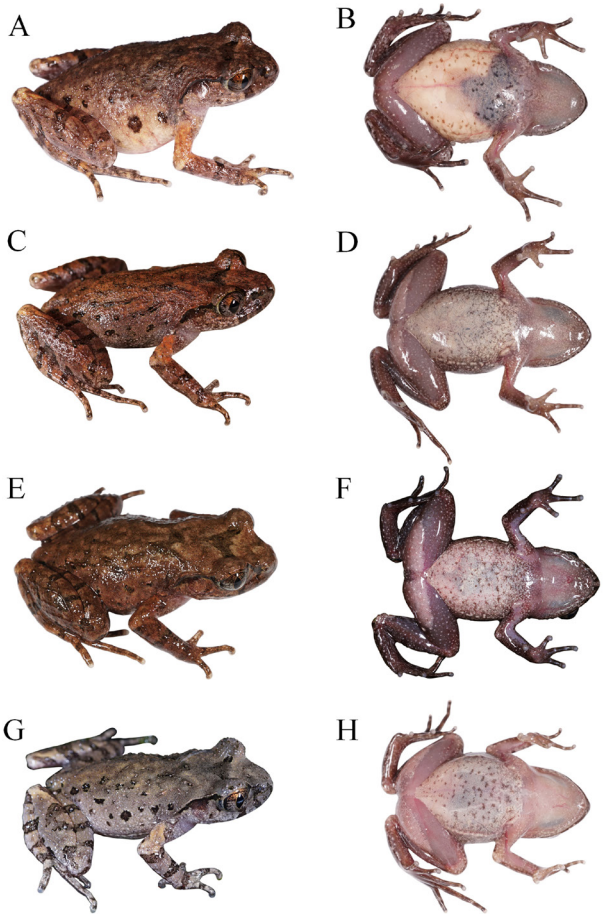

Figure 13 Photos showing colour variations in paratypes of *Leptobrachella yeae* sp. nov. A, B dorsolateral and ventral views of adult female CIBEM1845, respectively. C, D dorsolateral and ventral views of adult male CIBEM1839, respectively. E, F dorsolateral and ventral views of adult male CIBEMS20190422HLJ1-6, respectively. G dorsolateral view of adult male CIB EMS20190422HLJ1-7. H ventral view of adult male CIBEM1843.

constant type E calls. Type A present in the calls of the holotype after interrupted, then following calls gradually become type E and constant. For type A, dominant frequency (4562.5 ± 139.8) Hz, calls contain (7.2 ± 1.1) pules and last (70.3 ± 12.2) ms, inter call interval (2488.0 ± 1268.3) ms, amplitude of pulses at beginning and end of call similar, rise at (29.7 ± 15.2) ms of call, (9000 ± 530.3) Hz and (14437.5 ± 187.5) Hz frequency harmonic 1 and 2. For call type E, dominant frequency 4831.9 ± 155.8 Hz, harmonic 1 and 2 (9252 ± 554.6) Hz, (14250.0 ± 265.2) Hz; calls contain (34.0 ± 7.8) pulses; calls relatively long, duration (544.5 ± 146.8) ms, inter-call interval (353.7 ± 361.3) ms; amplitude of pulses at beginning and end of call similar, rise at (62.4 ± 36.9) ms.

Tadpoles. Figures 8B and 14. Measurements see Table S2. Measurements in mm. Description based on sequenced tadpole CIBEMS20190422HLJ1-1 at Gosner stage 36 (BL 17.7). Body elliptical elongate in dorsal view, widest at level of heart, slightly depressed BH 135% of BW; large lateral lymphatic sacs present; snout rounded, SN 23% of BL; eyes relatively, ED 8.2% of BL; pineal ocellus and nasolacrymal ducts invisible; nostrils near oval, moderate large, nostrils near oval, moderate large, rimed by four and three small lobes on left and right side, slightly closer to pupil than tip of snout, RN 110% of NE; PP 104% of IND; spiracle short, SS 52% of BL. Tail long and strong, TAL 243% of BL, TWH 82% of BH, TMW 55% BW; upper fin SU 136% of BL, slowly rise from proximal eighth of tail, extending to tip of tail, highest at distal third and smooth; lower fin attached to anal tube, smoothly higher, highest at distal third of tail, reaches tip of tail, LF 84% of UF; anal tube moderately sized, open on right side; glands on body invisible. Lateral line system (Figure 14 D): Generally similar with lateral system of *L. oshanensis*, but angular line contact orbit, dorsal and middle body line indistinct on body and tail.

Oral disc (Figure 8 B): relatively small, in shape of cup, transversely elongate, positioned and orient ventrally, not emarginated laterally, ODW 22% of BL and 51% of BW; lower labium divided, upper labium slightly concave in the middle; small papillae on margin around oral disc present above level of corner of mouth, absent on lower region; two and one submarginal papillae present laterally to keratodont rows of the lower labium and anteromedially to row P3 on left and right side respectively; KRF I:2+2/2+2:I, keratodont rows short, A2 > A3 > A1; first row on upper labium shortest, near oval, the second slightly interrupted, the third rows separated by upper

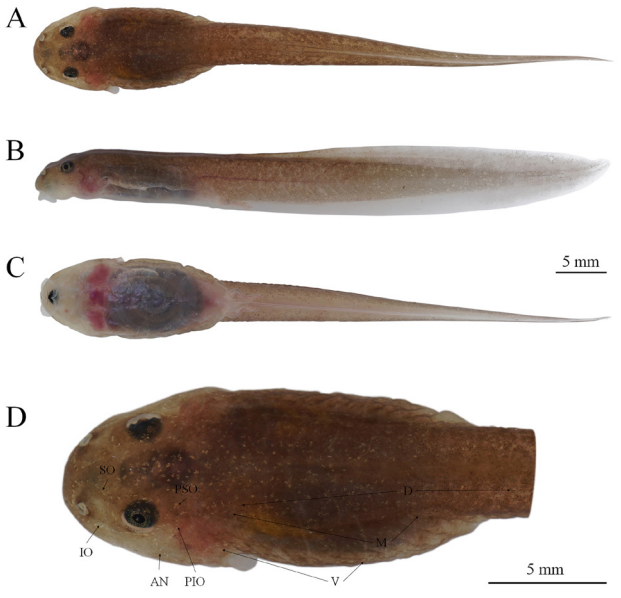

Figure 14 Photos of the tadpole CIBEMS20190422HLJ1-1 of *Leptobrachella yeae* sp. nov. in life. A: dorsal view. B: lateral view. C: ventral view. D: dorsolateral view of head. Abbreviations for characters: AN, angular; IO, infraorbital; SO, supraorbital; PIO, posterior infraorbital; PSO, posterior supraorbital; D, M, and V, dorsal, middle, and ventral body lines, respectively.

beak; P1 > P2 > P3; P3 very short, one-third of P1; P2 about half of P1. Keratodonts scythe blade shaped. Jaw sheaths strong, coarsely serrated.

Coloration in life (Figure 14). Dorsal body and tail muscle translucent light brown, dorsal body covered with copper specking; fins transparent covered with light brown iridophores on upper fin, lower fin without iridophores. Iris copper. Lateral sacs and ventral body transparent.

Coloration in preserve. Dorsal body and tail muscle pale brown; ventral part and fins transparent.

Variation. Figure 13. Measurements of paratypes see Table S1 (in mm). Skin texture of most paratypes relatively smooth with tiny granules, A total of eleven of 21 individuals covered few fine short granular ridges (CIBEM1840, CIBEM1841, CIBEM1843, CIBEM1846, CIBEM1851, CIBEM1853, CIBEM1855, CIBEM1856, CIBEM1858-CIBEM1860). Outer palmar tubercle with diameter about, larger or smaller than half of the inner. Pectoral glands of most specimens indistinct and flat (except CIBEM1846). Ventrolateral line most indistinct (except six individuals: CIBEM1849, CIBEM1853, CIBEM1854, CIBEM1858-CIBEM1860), present in interrupted or connected glandular line. Coloration variations. The dorsal color of examined specimens with deep, orange brown, or greyish brown. The brown "V" shaped pattern on snout indistinct or absent on most individuals; triangular pattern between upper eyelids present on all individuals; markings on shoulders present on most individuals, some irregular (Figure 13 A, C); no longitudinal stripes along dorsolateral body. Primary color on dorsal limbs similar with dorsal body; dorsal upper arm and tibiotarsal articulation generally brighter, brown or orange on deep brown colored individuals, yellow on greyish brown colored individuals, and orange on the orange brown colored. Deep color under supratympanic fold varies from covering most part of tympanum to upper edge of tympanum. Dark patches on flanks vary in shape and size, mostly with diameter larger than half of tympanum. Mostly three or four, seldomly two or no cross bands present on dorsal thigh. Ventral body basically cream, most pinkish, with brown specking on entire chest and upper and lateral belly or entire belly. Ventral thigh mostly pinkish, some purplish (Figure 13 F), light greyish black patches on posterior thigh present only around vent or absent. Pectoral glands and femoral glands colored similar with belly; humeral glands mostly buff, few brown, greyish brown or cream. The linea musculina cream white when present.

Skull variations. Four sequenced specimens were scanned, two adult females CIBEMLGL19052104, CIBEM1845 and two adult males CIBEMS20190422HLJ2-1, CIBEMS20190422HLJ1-6. The skulls of three paratypes generally resemble the holotype. Female paratype CIBEMLGL19052104 with a large anterior fontanelle; prootic completely contact with exoccipital (so as in other two paratypes scanned); quadratojugal weak, not overlap with maxillary. The base of nasal of CIBEMS20190422HLJ1-6 partially contact with sphenethmoid.

Measurements variation of tadpoles see Table S2. KRF mostly I: 3+3/2+2: I except one (CIBSC070) I: 3+3/3+3: I. Eyes smaller on tadpoles in earlier stage. Lower labium margin on CIBEMS20190422HLJ1-3 at stage 26 with papillae.

Comparisons. In *Leptobrachella*, 26 species occurring south of the Isthmus of Kra, and *Leptobrachella yeae* sp. nov. could be easily distinguished from them by several characters. By having supra-axillary and ventrolateral glands, the new species differs from *L. arayai*, *L. dringi*, *L. fritinniens*, *L. gracilis*, *L. hamidi*, *L. heteropus*, *L. kajangensis*, *L. kecil*, *L. marmorata*, *L. maura*, *L. melanoleuca*, *L. picta*, *L. platycephala*, *L. sabahmontana*, and *L. sola* (vs. absent in the latter). By having rounded fingertips, and moderate body size (25.8–32.6 mm in male, 33.7–34.1 mm in female), the new species differs from the following species with pointed fingertips and smaller body size: *L. baluensis* (14.9–15.9 mm in males), *L. bondangensis* (17.8 mm in male), *L. brevicrus* (17.1–17.8 mm in males), *L. fusca* (16.3 mm in male), *L. itiokai* (15.2–16.7 mm in males), *L. juliandringi* (17.0–17.2 mm in males), *L. mjobergi* (15.7–19.0 mm in males), *L. natunae*(17.6 mm in one adult male), *L. palmata* (14.4–16.8 mm in males), *L. parva* (15.0–16.9 mm in males), and *L. serasanae* (16.9 mm in female).

Leptobrachella yeae sp. nov. could also be identified from 54 known *Leptobrachella* species occurring north of the Isthmus of Kra by some characters (Table 4).

For species of *L. applebyi* species group *L. applebyi*, *L. ardens*, *L. bidoupensis*, *L. maculosa*, *L. melica*, *L. pallida*, *L. pyrrhops*, *L. rowleyae*, *L. tadungensis*, the new species differ by ventral body cream white with small brown specking on sides and upper abdomen (vs. basically reddish brown, brown, or pinkish milk-white, with white specking). The new species differ from *L. kalonensis* by fringes on toes narrow (vs. absent), differ from *L. petrops* by skin relatively smooth (vs. highly tuberculate)

Leptobrachella yeae sp. nov. differs from *L. laui*, *L. liui*, *L. yingjiangensis*, *L. yunkaiensis*, and *L. nyx* by having narrow fringes on toes (vs. with wide fringes in the latter and *vs.* without fringes in *L. ventripunctata*); differs from *L. tengchongensis*, *L. feii*, and *L. sungi* by body size moderate (25.8–32.6 mm in male in the new species *vs.* < 26.0 mm in the first two latter species and > 48.3 mm in *L. sungi*); differs from *L. pelodytoides* and *L. sungi* by toes webbing with rudimentary (vs. wide in the latter); differs from *L. tengchongensis*, *L. ventripunctata*, and *L. feii* by belly cream white with small brown specking on sides and upper abdomen (vs. with black spots or blotches in the latter); differs from *L. maoershanensis*, *L. tengchongensis*, *L. ventripunctata*, *L. wuhuangmontis*, *L. yingjiangensis*, *L. yunkaiensis*, *L. flaviglandulosa*, and *L. feii* by dorsal skin relatively smooth with tiny granules (vs. shagreened or rough with tubercles

or/and longitudinal skin ridges in the latter); differs from *L. maoershanensis*, *L. wuhuangmontis* and *L. yunkaiensis* by dermal ridges present under toes interrupted at the articulations (vs. uninterrupted in the latter).

Leptobrachella yeae sp. nov. differs from 20 species by moderate body size (males 25.8–32.6 mm, females 33.7–34.1 mm *vs.* 40.8 mm in male of *L. nahangensis*, 21.3–22.3 mm in *L. pluvialis* males, 45.8–52.5 mm in *L. zhangyapingi* males, 35.4–36.3 mm in two adult females of *L. neangi*); narrow lateral fringes on toes (absent in *L. crocea*, *L. lateralis*, *L. macrops*, *L. minima*, *L. namdongensis*, *L. nahangensis*, *L. neangi*, *L. pluvialis*, *L. tuberosa*; wide in *L. aerea*, *L. firthi*, *L. isos*, *L. nahangensis*, *L. khasiorum*, *L. tamdil*, and *L. zhangyapingi*); rudimentary webbing between toes (vs. wide in *L. tamdil*); dorsal skin relatively smooth with tiny granules (vs. shagreened or tuberculate in *L. aerea*, *L. botsfordi*, *L. crocea*, *L. firthi*, *L. khasiorum*, *L. lateralis*, *L. macrops*, *L. namdongensis*, *L. neangi*, *L. nokrekensis*, and *L. tuberosa*); belly cream white with small brown specking on sides and upper abdomen (vs. reddish brown in *L. botsfordi*; bright orange in *L. crocea*; white with brown dusting in *L. fuliginosa*; greyish-violet with white speckling in *L. macrops*; belly transparent, immaculate purplish gray in *L. neangi*; dirty white with dark brown marbling in *L. pluvialis*, reddish brown with white dusting in *L. puhoatensis*); black spots on flanks present (vs. absent in *L. aerea*, *L. botsfordi*, *L. crocea*, *L. firthi*, *L. isos*, *L. tuberosa*, *L. zhangyapingi*); iris bicolored, copper above, silver bellow; (vs. uniformly bronze in *L. aerea*, uniformly dark brownish gold in *L. botsfordi*; bright gold in *L. firthi*; reddish orange in upper half in *L. fuliginosa*; gold in *L. isos*; upper third bright orange, rest yellowish-cream in *L. khasiorum*; dark gold above, grey below in *L. minima*; uniformly gold in *L. nahangensis*; iris coppery orange around pupil, not distinctly bicolored in *L. neangi*; upper part reddish orange in *L. nokrekensis*; top third of iris bright orange in *L. tamdil*); moderate dominant frequency (4.6–4.8 kHz at 15–22 °C *vs.* 2.3-2.4 kHz at 19.3–19.6 °C in *L. fuliginosa*, 5.9–6.2 kHz at 22.4–22.8 °C in *L. isos*, 4.9–5.6 kHz at 22.3–25.8 °C in *L. puhoatensis*, 2.6–2.8 kHz at 22.5–24.5 °C in *L. tuberosa*).

Leptobrachella yeae sp. nov. was clustered into a big clade also containing ten phylogenetically related species, i.e., *L. alpina*, *L. purpurus*, *L. suiyangensis*, *L. purpuraventra*, *L. bijie*, *L. chishuiensis*, *L. niveimontis*, *L. bourreti*, *L. wulingensis*, and *L. eos*.

Leptobrachella yeae sp. nov. differs from sympatric and phylogenetically related congener *L. oshanensis* by fringes on toes narrow (vs. absent), dermal ridges under toes interrupted (vs. uninterrupted); dorsal skin relatively smooth with tiny granules (vs. shagreened, with fine dense granules and glandular ridges); dorsal body deep, yellowish or orange brown (vs. mostly uniformly reddish brown); distinct large greyish black patches on posterior thigh absent (vs. present); nasals of males entirely or partially separated from sphenethmoid (vs. completely in contact with the nasal contact with sphenethmoid in males); dorsal surface of tadpoles translucent light brown (vs. dorsal surface rufous). Advertisement call of the new species are simple, call series mainly consist of long or short repeated notes (vs. calls of *L. oshanensis* are complex, and its primary call contains three type, consist of different combination of short and relatively long notes). The new species emit calls with higher dominant frequency (4.6–4.8 kHz at 15–22 °C *vs.* 4.0–4.5 kHz at 19–22 °C in *L. oshanensis*). For the repeated long call (type E) and repeated short call (Type A) shared by these two species, the calls of the new species possess harmonics with higher frequency, longer call duration and note rise time. For type E calls, call intervals are shorter in the new species, and its pulses for the first note in a call are fewer than that of *L. oshanensis* (See comparisons and details in Table 5 and Table S4).

Leptobrachella yeae sp. nov. differs from phylogenetically related congener *L. alpina* by lateral fringes on toes narrow (vs. wide), belly cream white with small brown specking on sides and upper abdomen (vs. with dark spots); dorsum without white tiny flecks (vs. present).

Leptobrachella yeae sp. nov. differs from phylogenetically related congener *L. purpurus* by lateral fringes on toes narrow (vs. wide); dorsal body deep, yellowish or orange brown (vs. purplish brown); dorsal skin relatively smooth with tiny granules (vs. dorsal skin shagreened and scattered with fine, round reddish tubercles); calls with higher dominant frequency (4.6–4.8 kHz at 15–22 °C *vs.* 4.3–4.5 kHz at 15.0 °C in *L. purpurus*).

Leptobrachella yeae sp. nov. differs from phylogenetically related congener *L. suiyangensis* by dorsal skin relatively smooth with tiny granules (vs. shagreened and scattered with fine, rounded granules and short longitudinal folds); dorsal body deep, yellowish or orange brown (vs. purplish brown); skins beneath supratympanic fold dark brown, including most part of tympanum and upper part of temporal (vs. tympanum is light brown-grey, lower edge of the upper drum ridge is prominently black).

Leptobrachella yeae sp. nov. differs from phylogenetically related congener *L. purpuraventra* by dermal ridges under toes interrupted at the articulations (vs. not interrupted); ventral body cream white (vs. ventral surface grey purple); dense tiny conical spines on surface of chest extending to anterior region of abdomen absent in males during breeding season (vs. present).

Leptobrachella yeae sp. nov. differs from phylogenetically related congener *L. bijie* by longitudinal ridges under toes interrupted at the articulations (vs. uninterrupted); dense tiny conical spines on surface of chest extending to anterior region of abdomen absent in males during breeding season (vs. present); internasal distance smaller than interorbital distance (vs. equal).

Leptobrachella yeae sp. nov. differs from phylogenetically related congener *L. chishuiensis* by internasal distance smaller

than interorbital distance (vs. larger); tibia-tarsal articulation reaches the middle eye when leg stretched forward (vs. reaches tympanum); dorsal body lighter colored and mostly yellowish or orange brown (vs. brown) calls with lower dominant frequency (4.6–4.8 kHz at 15–22 °C *vs.* 6.1–6.3 kHz at 20 °C).

Leptobrachella yeae sp. nov. differs from phylogenetically related congener *L. niveimontis* by larger body size (males 25.8–32.6 mm *vs.* 22.5–23.6 mm); cream white with small brown specking on sides and upper abdomen (vs. marbling with black speckling); dermal ridges present under toes interrupted at the articulations (vs. uninterrupted).

Leptobrachella yeae sp. nov. differs from phylogenetically related congener *L. bourreti* by relatively smaller body size (males 25.8–32.6 mm *vs.* 28.0–36.2 mm); dermal ridges under toes distinct (vs. poorly developed); dermal fringes on fingers absent (vs. fngers II and III with dermal fringe); nostrils closer to tip of snout than eye (vs. reverse); interorbital space larger than upper eyelid (vs. equal).

Leptobrachella yeae sp. nov. differs from phylogenetically related congener *L. wulingensis* by dorsal skin relatively smooth with tiny granules (vs. dorsal skin shagreened with sparse, large warts, sometimes with longitudinal ridges); dorsal body deep, yellowish or orange brown (vs. brown); dense small white conical spines on lateral and ventral surface of tarsus, surface of tibia-tarsal, inner-side surface of shank absent (vs. present); relative finger lengths I < II < IV < III (vs. I < II = IV < III).

Leptobrachella yeae sp. nov. differs from phylogenetically related congener *L. eos* by smaller body (males 25.8–32.6 mm *vs.* 33.1–34.7 mm); toes with narrow lateral fringes (vs. with well-developed fringes); dorsal skin relatively smooth (vs. shagreened); dorsal pattern distinct (vs. poorly distinct); black spots on flanks present (vs. absent); copper above, silver bellow (vs. iris orange above, light golden below).

Etymology. The specific epithet "yeae" is in honor of Changyuan Ye for her contribution on herpetology. We suggested common name as "Ye's leaf litter toad", and Chinese name as "Ye Shi Zhang Tu Chan (叶氏掌突蟾)".

Distribution and ecology. *Leptobrachella yeae* sp. nov. is known from Emei Mountain, Sichuan Province, China. This species is common at its distribution area. It was found calling under dense herb leaves beside montane streams in broad leaf forest from April 20 to May 5, recorded at elevation between 783 m to 1806 m (Figure 14 B). Tadpoles of *Leptobrachella yeae* sp. nov. were collected from the same stream pond where tadpoles of *L. oshanensis* at Heilongjiang river. Males often heard calling in packs around a small section of stream. This species was recorded to co-occur with *L. oshanensis* only in near Qingyinge of Heilongjiang River. Seven species of Megophryidae were recorded to be sympatric: *L. oshanensis*, *Megophrys omeimontis*, *M.* cf. *minor*, *Leptobrachium boringii*, *Oreolalax omeimontis*, *O. major*, and *O. popei*.

4. Discussion

Superficially morphological similarity between species of the toad group *Leptobrachella* severely masked the new species though numerous herpetological surveys have been conducted on Emei Mountain since 1950. Deeply based on molecular phylogenetic evidence, several new species have been described in *L. oshanensis* species complex (e.g., Lyu *et al.* 2019; Chen *et al.*, 2020; Li *et al.*, 2020). *Leptobrachella yeae* sp. nov. and *L. oshanensis* can be distinguished from each other by highly different advertisement calls, highlighting the importance of advisement call in species identification in the genus.

Sexual dimorphism skin glands (SDSG) of amphibians are macroglands that mediate amphibian social communication and reproductive patterns, and it has been proved to be capable for producing proteinaceous sexual pheromones which is believed to attract females at male calling based on the histochemistry and behavior evidence (Thomas *et al.*, 1993; Gong *et al.*, 2020). In this paper, we described first known SDSG of Megophryidae, the femoral adipose glands (Fei *et al.*, 2009; Fei and Ye, 2016; other literatures in Table 2; specimens examined in Appendix). This gland present in the clade including 12 species: *L. alpine* (examined specimens in Appendix), *L. bijie* (examined specimens in Appendix I), *L. bourreti* (e.g. Figure 12 B of Ohler *et al.*, 2011), *L. chishuiensis* (e.g. Figure 6 C D of Liu *et al.*, 2020), *L. eos* (examined specimens in Appendix), *L. niveimontis* (Figrue 5 B2 of Chen *et al.*, 2020), *L. oshanensis* (examined specimens), *L. purpuraventra* (examined specimens in Appendix), *L. purpurus* (e.g. Figure 2 C of Yang *et al.*, 2018), *L. suiyangensis* (examined specimens in Appendix), *L. tengchongensis* (Figure 5 C of Yang *et al.*, 2016), *L. wulingensis* (examined specimens in Appendix, note that adult males collected in September without femoral adipose glands, , see in Figures 3 C, 4 K–N in Qian *et al.*, 2020). Thus, considering *L. oshanensis* was firstly described among these species, we propose this clade as *L. oshanensis* species group. The species group differs from most species of other clades that do not possess femoral adipose glands, such as *L. liui*, *L. wuhuangmontis*, *L. laui*, *L. mangshanensis* and *L. yunkaiensis* (examined specimens in Appendix). The femoral adipose glands could be nonperennial. Based on observation on a population of *L.* cf. *wulingensis* (unpublished data), adult males collected in September (nonbreeding season) without femoral adipose glands, and the glands faded after breeding males were kept in lab for a month. The function of the femoral adipose glands was assumed to involve with breeding but the mechanism was not clear.

The discovery of *Leptobrachella yeae* sp. nov. made the species

number of the genus *Leptobrachella* in China to 26, including the new species, *L. alpina*, *L. bourreti*, *L. bijie*, *L. chishuiensis*, *L. eos*, *L. feii*, *L. flaviglandulosa*, *L. laui*, *L. liui*, *L. mangshanensis*, *L. maoershanensis*, *L. niveimontis*, *L. nyx*, *L. oshanensis*, *L. pelodytoides*, *L. purpurus*, *L. purpuraventra*, *L. shangsiensis*, *L. sungi*, *L. tengchongensis*, *L. ventripunctata*, *L. wuhuangmontis*, *L. yingjiangensis*, and *L. yunkaiensis* (Chen *et al.*, 2020; Frost, 2020; Li *et al.*, 2020; Lyu et al., 2020). These findings further proved the widely recorded species *L. oshanensis* as a species complex. Yet, there are still cryptic species distribute at where *L. oshanensis* were recorded (Chen *et al.*, 2018). Future deep surveys in these areas are therefore expected.

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Appendix

Specimens examined.

Leptobrachella alpina: An adult female SYS a003927, collected from type locality Huangcaoling, Jingdong County, Yunnan Province, China. The adult male holotype, CIB 873148.

Leptobrachella bijie: Type specimens. 3 adult males SYSa007314–16. collected from Guizhou Province, China.

Leptobrachella purpuraventra: Type series. 2 adult females, SYSa007278, SYSa007304; 3 adult males SYSa007284, SYSa007280, SYSa007282. All collected from Guizhou Province, China.

Leptobrachella yunkaiensis: Type series. 3 adult males, SYSa004669, SYSa004667, SYSa004665; 2 adult females, SYSa004663, SYSa004690. All collected from Maoming City, Guangdong Province, China.

Leptobrachella wuhuangmontis: Type series. 2 adult males, SYSa003481, SYSa003505; 2 adult females, SYSa003485, SYSa003499. Collected from Mt. Wuhuang, Guangdong Province, China.

Leptobrachella laui: Type series. An adult male SYSa002058 from Hongkong, China.

Leptobrachella mangshanensis: 3 adule males SYSa002828, SYSa002827, SYSa002830 from Nanling Mountains, Guangdong Province, China. 4 unvouchered adult males from type locality Mt. Mangshan, Hunan Province, China.

Leptobrachella eos: 7 adult males SYSa003959, CIB MLMY20170815–17, CIB MHKA20170806-8 from Mengla, Yunnan Province, China.

Leptobrachella ventripunctata: 2 adult males SYSA003957, SYSA003958 from type locality Zhushihe, Mengla, Yunnan Province, China. 8 adult males CIB MLML20170802–9 from Manla, Mengla, Yunnan Province, China.

Leptobrachella liui: 6 adult males, CIB83489–91, CIB83493–5; one adult female CIB83492 collected from type locality Mt. Wuyi, Fujian Province, China.

Leptobrachella suiyangensis: one adult male CIB WB2020210 from Tongzi, Guizhou Province, China. Identified with 16S rRNA sequence. Collected when calling.

Leptobrachella wulingensis: 3 adult males CIB TPS2019041339, CIB TPS20190413MW1, CIB TPS20190412Z3; 3 adult females CIB TPS20190412Z21, CIB TPS20190413MW2, CIB TPS2019041117 from Mt. Tianping, Sangzhi, Hunan Province, China. 4 adult males TZS2019041101–4, from type locality Mt. Tianzishan, Hunan Province, China. All males collected when calling.

Table S1 Measurements of *Leptobrachella yeae* sp. nov. and *L. oshanensis*. Units in mm. See abbreviations for characters in the Materials and Methods section.

Species	Voucher No.	Sex	Status	SVL	HDL	HDW	SNT	EYE	IOD	IN	UEW	SL	NS	TMP	TYE	HAL	FLL	FLW	FL	TL	TW	FOL	TFOL	PEC	FEM	HUM	FTN
Leptobrachella yeae sp. nov.	CIBEMS20190422HLJ2-1	Male	**Holotype**	28.8	9.8	9.2	3.7	3.2	3.2	3.0	2.4	2.2	1.8	1.9	1.2	7.3	6.8	2.2	13.2	14.1	3.5	13.1	20.2	1.6	0.8	0.8	6.0
Leptobrachella yeae sp. nov.	CIBEMS20190422HLJ1-6	Male	Paratype	31.2	11.8	10.9	4.4	3.8	3.5	3.3	2.9	2.2	1.9	2.2	1.2	7.1	6.7	2.6	13.6	13.7	3.8	12.6	20.2	1.6	0.7	0.4	5.6
Leptobrachella yeae sp. nov.	CIBEMS20190422HLJ1-7	Male	Paratype	29.62	11.1	10.51	4.73	3.78	3.33	3.27	2.78	2.28	1.86	1.77	1.34	6.96	6.48	2.27	13.15	13.71	3.68	12.46	20.03	1.29	0.4	0.46	5.09
Leptobrachella yeae sp. nov.	CIBEMS20190422HLJ1-8	Male	Paratype	25.8	9.2	8.8	4.1	3.3	3.1	2.7	2.3	1.9	1.7	1.7	1.0	6.8	6.0	1.9	12.3	12.8	2.8	11.8	18.8	1.4	0.7	0.7	5.0
Leptobrachella yeae sp. nov.	CIBEM1839	Male	Paratype	28.8	10.27	9.98	4.22	3.49	2.96	3.19	2.44	2.21	1.93	1.91	1.2	6.84	6.66	2.03	13.07	14.02	3.27	13.41	20.93	1.44	0.69	0.29	5.29
Leptobrachella yeae sp. nov.	CIBEM1840	Male	Paratype	27.2	10.1	9.5	4.0	3.2	3.0	3.2	2.6	2.0	1.8	1.7	1.3	6.9	6.1	1.9	12.8	13.2	3.4	12.3	19.1	1.1	0.6	0.5	5.4
Leptobrachella yeae sp. nov.	CIBEM1841	Male	Paratype	28.67	10.54	9.84	4.01	3.19	3.26	3.05	2.45	2.34	1.73	1.81	1.21	7.64	7.04	2.08	13.53	14.68	3.25	14.24	21.96	1.02	0.58	0.65	5.71
Leptobrachella yeae sp. nov.	CIBEM1842	Male	Paratype	27.9	11.0	10.8	4.2	3.6	3.2	2.9	2.7	2.2	1.9	1.7	1.1	6.8	6.5	2.3	13.2	14.0	3.6	12.0	19.1	1.0	0.6	0.4	5.9
Leptobrachella yeae sp. nov.	CIBEM1844	Male	Paratype	29.2	9.76	9.37	4.12	3.6	3.04	3.12	2.73	2.03	1.88	1.73	0.98	7.01	7.27	2.18	13.15	13.53	3.52	13.26	20.71	1.05	0.69	0.24	5.77
Leptobrachella yeae sp. nov.	CIBEM1849	Male	Paratype	30.1	10.4	10.2	4.0	3.6	3.2	2.9	3.0	2.3	1.7	1.9	1.1	7.4	7.0	2.2	13.2	14.2	3.7	13.2	21.0	1.2	0.9	0.6	5.7
Leptobrachella yeae sp. nov.	CIBEM1845	Female	Paratype	34.06	12.13	11.41	4.48	4.14	3.69	3.37	2.73	2.36	2.12	2.08	1.44	8.21	7.61	2.02	14.47	15.38	3.9	14.72	23.42	/	1.2	0.9	6.73
Leptobrachella yeae sp. nov.	CIBEMLGL19052104	Female	Paratype	33.7	11.0	10.4	4.5	3.6	3.9	3.3	2.7	2.9	1.9	2.0	1.2	7.9	7.3	2.0	14.8	14.9	3.5	14.1	22.7	1.2	1.0	0.8	6.3
L. oshanensis	CIB24358 (A1000)	Male	Holotype	26.5	10.2	9.1	3.6	3.3	2.6	2.5	2.2	2.1	1.5	2	1.5	6.7	5.67	1.8	11.9	11.8	3.2	11.9	18.2	/	0.8	0.8	5.2
L. oshanensis	CIBEMS20190421SSG1-9	Male	Topotype	30.4	11.0	10.9	4.0	3.4	3.3	2.9	2.8	2.5	1.7	1.6	1.4	7.8	6.8	2.4	14.2	14.8	3.5	13.7	22.0	1.2	0.6	1.1	5.5
L. oshanensis	CIBEMS20190421SSG1-11	Male	Topotype	28.55	10.06	9.01	3.63	3.49	3.15	2.86	2.5	2.2	1.76	1.87	1.28	7.67	6.57	2.15	13.47	13.92	3.56	12.01	20	0.93	0.61	0.82	5.89
L. oshanensis	CIBEMS20190422SSG2-1	Male	Topotype	29.5	10.4	9.9	4.0	3.8	3.2	3.1	2.7	2.2	1.7	1.9	1.2	7.2	7.0	2.0	12.5	13.6	3.3	12.9	20.7	1.4	0.7	0.8	5.4
L. oshanensis	CIBEMS20190422SSG3-1	Male	Topotype	29.67	10.8	9.98	4.25	3.58	3.02	2.63	2.71	2.08	1.87	1.71	1.02	7.2	7.3	2.08	13.41	14.24	3.53	14.55	21.21	1.21	0.84	0.74	6.24
L. oshanensis	CIBEMS20190422SSG4-1	Male	Topotype	29.1	11.4	10.0	4.0	3.7	3.0	2.8	2.7	2.4	1.9	1.8	1.2	7.2	7.2	2.5	13.2	14.1	3.6	12.9	20.6	1.1	0.8	1.0	5.8
L. oshanensis	CIBEMS20190421BGS5	Male	Topotype	26.7	9.34	9.32	3.85	3.56	2.98	2.94	2.41	2.26	1.78	1.91	1.34	6.64	6.05	1.97	12.04	12.35	2.95	11.42	18.47	1.01	0.55	0.72	4.97
L. oshanensis	CIBEMS20190421BGS6	Male	Topotype	27.8	10.3	10.3	4.0	3.6	3.0	3.3	2.5	2.5	1.4	2.1	1.3	6.8	6.6	2.2	13.4	13.8	3.5	12.3	19.8	1.4	0.8	0.4	5.7
L. oshanensis	CIBEMS20190421BGS7	Male	Topotype	30.52	11.92	10.55	4.43	3.53	3.46	3.26	2.64	2.81	1.83	2.06	1.51	7.18	7.4	2.51	14.27	14.45	3.73	13.16	20.94	1.19	0.62	0.51	5.98
L. oshanensis	CIBEMS20190421BGS8	Male	Topotype	29.2	10.2	10.3	4.3	3.7	3.2	2.8	2.7	1.9	2.0	1.8	1.5	6.9	7.0	2.2	13.9	13.9	3.7	12.6	20.0	1.3	1.0	0.6	5.7
L. oshanensis	CIBEMS20190421BGS9	Male	Topotype	27.68	10.26	9.67	3.96	3.75	3.26	2.96	2.54	2.22	1.57	2.04	1.15	6.67	6.53	1.86	12.85	13.18	3.29	11.69	18.98	1.35	1.13	0.5	6
L. oshanensis	CIBEMS20190421SSG1-8	Female	Topotype	32.6	11.0	10.7	4.5	4.0	3.4	3.1	3.1	2.7	1.9	2.3	1.3	7.9	7.6	1.8	14.6	15.0	3.2	13.5	22.4	1.2	0.8	1.0	6.4
L. oshanensis	CIBEMS20190421SSG1-10	Female	Topotype	28.8	10.06	9.41	4.25	3.45	3.32	2.67	2.57	2.05	1.61	1.92	1.19	6.74	7.09	1.83	12.21	12.94	2.94	11.74	19.01	0.37	0.42	0.54	5.93

Table S2 Measurements of tadpoles of *Leptobrachella yeae* sp. nov. and *L. oshanensis*. Units in mm. See abbreviations for morphometric characters in Materials and Methods section.

Species	Vochuer	Gonser stage	BH	BL	BW	ED	PP	NE	IND	SN	RN	SS	SU	ODW	TAL	UF	LF	TMW	TMH	BH/BW	ED/BL	RN/NE	PP/IND	SN/BL	SS/BL	TAL/BL	TMH/BH	TMW/BW	SU/BL	LF/UF	ODW/BW	ODW/BL
Leptobrachella yeae sp. nov.	CIBEM1867	37	5.0	17.6	7.5	1.6	4.3	1.9	3.4	3.9	1.8	7.8	19.3	3.8	39.9	2.3	1.9	4.0	4.7	150%	9.2%	98%	126%	22%	44%	226%	95%	53%	109%	85%	50%	21%
Leptobrachella yeae sp. nov.	CIBEMS20190422HLJ1-1	36	5.8	17.7	7.8	1.5	3.5	1.8	3.4	4.1	2.0	9.2	24.0	3.9	42.9	2.2	1.8	4.3	4.8	135%	8.2%	110%	104%	23%	52%	243%	82%	55%	136%	84%	51%	22%
Leptobrachella yeae sp. nov.	CIBEMS20190422HLJ1-3	26	4.5	14.3	6.1	0.8	2.5	1.5	2.4	3.3	1.7	6.5	18.3	3.2	28.1	1.8	1.6	3.2	3.8	134%	5.5%	113%	102%	23%	45%	197%	85%	52%	128%	87%	52%	22%
Leptobrachella yeae sp. nov.	CIBSC066	28	6.0	17.3	7.8	0.9	3.1	1.8	2.7	4.1	2.3	7.5	21.1	4.0	35.2	1.9	1.5	3.7	4.5	131%	5.3%	128%	112%	23%	44%	204%	76%	47%	122%	76%	51%	23%
Leptobrachella yeae sp. nov.	CIBSC068	26	4.7	14.4	6.6	0.7	2.6	1.6	2.5	3.4	1.8	6.6	16.0	3.2	32.8	1.6	1.7	3.2	3.5	140%	4.6%	116%	104%	23%	45%	227%	75%	48%	111%	107%	48%	22%
Leptobrachella yeae sp. nov.	CIBSC069	26	5.4	16.1	8.0	0.8	2.9	1.6	2.7	3.5	2.0	7.3	22.2	3.7	35.6	1.7	2.0	3.8	4.9	148%	4.6%	124%	107%	21%	45%	221%	90%	48%	137%	116%	46%	23%
Leptobrachella yeae sp. nov.	CIBSC070	36	6.1	18.6	8.7	1.2	3.5	2.0	3.2	4.2	2.4	7.8	23.2	4.6	40.2	2.5	2.1	4.5	4.9	142%	6.5%	124%	109%	22%	42%	217%	81%	52%	125%	86%	54%	25%
Leptobrachella yeae sp. nov.	CIBSC071	26	4.7	16.1	6.6	1.0	3.1	2.0	2.8	3.8	1.9	7.3	18.4	3.1	36.1	2.0	2.0	3.5	4.0	140%	5.9%	95%	108%	24%	45%	224%	86%	53%	114%	97%	48%	19%
Leptobrachella yeae sp. nov.	CIBSC072	25	3.5	12.9	4.7	0.4	2.4	1.7	2.4	2.7	1.5	5.8	13.0	2.9	27.6	1.5	1.4	2.9	3.5	134%	3.3%	88%	100%	21%	45%	214%	101%	61%	101%	95%	62%	23%
L. oshanensis	CIBEMS20190422SSG1-1	34	5.3	18.6	8.4	1.5	3.8	1.7	3.3	4.1	2.5	8.7	24.0	4.7	38.8	2.3	1.5	4.9	4.7	160%	7.8%	148%	115%	22%	47%	209%	90%	58%	129%	64%	55%	25%
L. oshanensis	CIBEMS20190422HLJ1-4	35	5.3	16.1	7.4	1.4	3.1	1.9	2.8	3.5	2.0	7.5	21.5	3.7	36.2	1.8	1.4	4.3	4.0	140%	8.7%	106%	111%	22%	46%	225%	76%	58%	134%	73%	50%	23%
L. oshanensis	CIBEMS20190422HLJ1-2	33	5.8	16.6	8.3	1.3	3.5	1.6	3.3	4.1	2.2	8.1	19.3	4.3	33.5	2.2	1.8	4.6	5.0	144%	7.8%	135%	104%	25%	49%	201%	86%	56%	116%	81%	52%	26%
L. oshanensis	CIBEMS20190421BGS1	35	5.2	18.1	7.6	1.5	3.3	1.9	2.8	4.0	1.8	8.4	23.1	4.1	42.5	2.6	2.0	4.5	4.8	148%	8.3%	96%	120%	22%	46%	235%	92%	59%	128%	77%	53%	23%
L. oshanensis	CIBEMS20190422SSG1-2	33	5.2	17.8	7.7	1.6	3.6	1.8	3.2	4.1	2.0	8.6	25.2	3.8	41.8	2.3	1.6	4.6	5.0	149%	9.0%	112%	113%	23%	48%	234%	96%	59%	141%	69%	50%	21%
L. oshanensis	CIBEMS20190422SSG1-3	31	4.7	15.6	6.2	1.3	3.2	1.8	2.9	3.8	1.9	7.9	18.3	3.8	34.1	2.1	1.3	3.9	4.7	132%	8.6%	108%	112%	24%	50%	219%	100%	63%	117%	64%	60%	24%
L. oshanensis	CIBEMS20190422SSG1-4	25	3.7	13.4	4.8	0.7	2.5	1.4	1.5	3.1	1.7	6.3	16.5	2.6	27.0	1.3	0.9	3.1	3.5	129%	5.4%	115%	173%	23%	47%	201%	95%	65%	123%	72%	53%	19%
L. oshanensis	CIBEMS20190422SSG3-2	36	5.9	18.3	7.9	1.6	3.0	2.0	3.0	4.1	2.6	8.6	23.9	4.0	44.3	2.2	1.8	4.8	5.1	135%	8.9%	132%	101%	23%	47%	242%	87%	61%	131%	82%	51%	22%
L. oshanensis	CIBSC062	34	5.2	17.6	7.6	1.3	3.5	1.7	3.0	4.4	2.4	8.3	20.1	4.1	39.8	2.1	1.6	4.4	5.0	146%	7.3%	138%	114%	25%	47%	226%	95%	58%	114%	75%	54%	23%
L. oshanensis	CIBSC063	34	5.1	18.1	7.6	1.3	3.7	2.0	3.2	4.2	2.3	8.6	22.3	4.2	40.3	2.4	1.7	4.6	4.9	149%	6.9%	113%	115%	23%	48%	223%	96%	60%	123%	72%	55%	23%
L. oshanensis	CIBSC064	35	6.3	17.8	8.6	1.4	3.3	1.9	3.0	4.4	2.5	8.4	25.1	4.2	43.0	2.3	1.7	4.5	5.4	137%	7.6%	133%	109%	25%	47%	241%	87%	53%	141%	74%	49%	23%

Table S3 Uncorrected *p*-distance between *Leptobrachella* species on the 16S gene.

No.	Species	1–21	22	23	24	25	26	27	28	29	30	31–53	54	55	56	57	58	59	60	61	62	63	64	65
1–21	*Leptobrachella yeae* sp.nov.	0.000–0.004
22	*L. alpinus*	0.055
23	*L. purpurus*	0.045	0.016
24	*L. suiyangensis*	0.050	0.051	0.045
25	*L. purpuraventra*	0.038	0.045	0.039	0.038
26	*L. bijie*	0.048	0.051	0.048	0.048	0.038
27	*L. chishuiensis*	0.052	0.049	0.051	0.046	0.028	0.018
28	*L. niveimontis*	0.047	0.053	0.041	0.057	0.047	0.049	0.055
29	*L. bourreti*	**0.037**	0.045	0.043	0.048	0.044	0.057	0.044	0.043
30	*L. wulingensis*	0.044	0.043	0.044	0.052	0.045	0.059	0.048	0.055	0.037
31–53	*L. oshanensis*	0.059	0.077	0.059	0.077	0.062	0.079	0.079	0.063	0.068	0.074	0.000–0.006
54	*L. eos*	0.053	0.057	0.034	0.064	0.053	0.069	0.072	0.049	0.048	0.046	0.063
55	*L. tengchongensis*	0.087	0.075	0.067	0.097	0.078	0.087	0.091	0.079	0.080	0.094	0.091	0.085
56	*L. puhoatensis*	0.106	0.104	0.105	0.115	0.110	0.124	0.097	0.106	0.105	0.099	0.109	0.105	0.080
57	*L. namdongensis*	0.098	0.098	0.090	0.111	0.098	0.110	0.101	0.086	0.100	0.094	0.107	0.085	0.072	0.054
58	*L. petrops*	0.108	0.106	0.097	0.111	0.110	0.124	0.105	0.104	0.106	0.104	0.116	0.097	0.076	0.059	0.065
59	*L. yingjiangensis*	0.096	0.091	0.082	0.115	0.088	0.102	0.098	0.099	0.096	0.088	0.096	0.087	0.079	0.099	0.098	0.078
60	*L. khasiorum*	0.130	0.126	0.120	0.143	0.140	0.147	0.132	0.124	0.113	0.124	0.120	0.115	0.099	0.105	0.111	0.096	0.094
61	*L. liui*	0.118	0.125	0.104	0.140	0.122	0.125	0.120	0.123	0.121	0.108	0.113	0.115	0.115	0.127	0.117	0.127	0.102	0.121
62	*L. mangshanensis*	0.134	0.102	0.118	0.121	0.136	0.142	0.112	0.107	0.133	0.121	0.125	0.116	0.123	0.126	0.124	0.133	0.125	0.149	0.030
63	*L. laui*	0.117	0.122	0.111	0.147	0.132	0.132	0.129	0.124	0.127	0.122	0.117	0.127	0.112	0.116	0.119	0.136	0.098	0.120	0.065	0.071
64	*L. maoershanensis*	0.110	0.104	0.093	0.124	0.102	0.118	0.110	0.108	0.112	0.096	0.104	0.100	0.106	0.105	0.101	0.111	0.091	0.115	0.083	0.061	0.090
65	*L. yunkaiensis*	0.090	0.097	0.087	0.108	0.090	0.106	0.100	0.091	0.094	0.090	0.094	0.092	0.100	0.104	0.098	0.106	0.083	0.109	0.079	0.065	0.081	0.067
66	*L. flaviglandulosa*	0.093	0.086	0.077	0.107	0.090	0.101	0.095	0.088	0.095	0.085	0.081	0.088	0.091	0.096	0.094	0.100	0.088	0.105	0.071	0.055	0.076	0.067	0.057
67	*L. sungi*	0.114	0.120	0.107	0.118	0.116	0.122	0.120	0.120	0.116	0.106	0.112	0.116	0.100	0.094	0.102	0.106	0.120	0.135	0.138	0.121	0.144	0.122	0.120
68	*L. zhangyapingi*	0.112	0.106	0.097	0.118	0.116	0.118	0.112	0.118	0.112	0.104	0.117	0.102	0.106	0.118	0.106	0.120	0.116	0.146	0.135	0.121	0.142	0.134	0.128
69	*L. isos*	0.129	0.122	0.125	0.130	0.142	0.150	0.131	0.128	0.119	0.122	0.139	0.133	0.104	0.127	0.119	0.133	0.133	0.149	0.150	0.167	0.165	0.146	0.140
70	*L. firthi*	0.132	0.131	0.127	0.140	0.147	0.146	0.132	0.125	0.120	0.131	0.140	0.134	0.114	0.121	0.119	0.130	0.144	0.131	0.142	0.160	0.157	0.156	0.140
71	*L. minimus*	0.109	0.100	0.100	0.109	0.110	0.122	0.095	0.104	0.098	0.107	0.107	0.108	0.091	0.099	0.097	0.105	0.116	0.113	0.127	0.136	0.129	0.103	0.105
72	*L. ventripunctatus*	0.110	0.110	0.101	0.126	0.112	0.118	0.110	0.112	0.116	0.106	0.119	0.114	0.110	0.112	0.098	0.122	0.118	0.146	0.127	0.114	0.141	0.120	0.115
73	*L. feii*	0.108	0.094	0.088	0.101	0.102	0.110	0.104	0.104	0.100	0.102	0.110	0.110	0.102	0.115	0.106	0.118	0.120	0.146	0.143	0.119	0.142	0.108	0.115
74	*L. aereus*	0.092	0.082	0.084	0.097	0.085	0.096	0.090	0.097	0.086	0.090	0.100	0.098	0.090	0.100	0.092	0.108	0.107	0.133	0.126	0.106	0.136	0.098	0.105
75	*L. wuhuangmontis*	0.120	0.117	0.119	0.127	0.124	0.138	0.114	0.117	0.111	0.115	0.121	0.118	0.119	0.121	0.118	0.129	0.133	0.143	0.124	0.141	0.143	0.113	0.109
76	*L. pluvialis*	0.100	0.101	0.093	0.100	0.090	0.106	0.092	0.103	0.094	0.098	0.102	0.100	0.100	0.100	0.102	0.108	0.106	0.134	0.115	0.094	0.129	0.092	0.091
77	*L. shangsiensis*	0.112	0.109	0.099	0.133	0.110	0.124	0.113	0.113	0.110	0.116	0.115	0.117	0.104	0.112	0.110	0.123	0.120	0.139	0.130	0.147	0.124	0.117	0.118
78	*L. nyx*	0.099	0.092	0.097	0.105	0.109	0.115	0.089	0.088	0.098	0.097	0.109	0.106	0.092	0.100	0.093	0.099	0.115	0.126	0.103	0.125	0.115	0.098	0.097
79	*L. nahangensis*	0.096	0.094	0.095	0.114	0.098	0.108	0.096	0.106	0.090	0.084	0.105	0.104	0.098	0.092	0.092	0.106	0.106	0.124	0.115	0.105	0.125	0.106	0.104
80	*L. kalonensis*	0.157	0.151	0.142	0.155	0.166	0.171	0.164	0.151	0.157	0.147	0.148	0.146	0.149	0.147	0.150	0.143	0.138	0.162	0.180	0.174	0.186	0.151	0.149
81	*L. bidoupensis*	0.155	0.143	0.137	0.150	0.148	0.153	0.153	0.140	0.151	0.137	0.145	0.140	0.141	0.135	0.141	0.141	0.131	0.153	0.159	0.141	0.171	0.140	0.145
82	*L. pallidus*	0.144	0.147	0.138	0.145	0.155	0.157	0.150	0.143	0.150	0.143	0.141	0.142	0.141	0.145	0.149	0.139	0.132	0.154	0.164	0.160	0.155	0.143	0.141
83	*L. tadungensis*	0.143	0.146	0.135	0.146	0.159	0.156	0.147	0.142	0.137	0.134	0.138	0.143	0.142	0.133	0.131	0.129	0.141	0.149	0.158	0.163	0.174	0.148	0.142
84	*L. macrops*	0.172	0.174	0.165	0.167	0.163	0.182	0.177	0.171	0.167	0.166	0.165	0.165	0.158	0.158	0.165	0.161	0.162	0.197	0.188	0.152	0.203	0.165	0.168
85	*L. pyrrhops*	0.156	0.166	0.154	0.171	0.172	0.183	0.172	0.164	0.158	0.155	0.161	0.148	0.155	0.156	0.152	0.145	0.146	0.155	0.176	0.181	0.174	0.148	0.156
86	*L. maculosus*	0.133	0.122	0.127	0.138	0.144	0.149	0.139	0.132	0.133	0.124	0.144	0.131	0.126	0.124	0.120	0.118	0.132	0.151	0.145	0.148	0.157	0.128	0.134
87	*L. melicus*	0.128	0.122	0.130	0.127	0.130	0.142	0.125	0.124	0.122	0.117	0.125	0.128	0.127	0.130	0.122	0.130	0.138	0.146	0.165	0.169	0.169	0.143	0.144
88	*L. applebyi*	0.144	0.141	0.139	0.145	0.153	0.159	0.141	0.143	0.141	0.133	0.132	0.140	0.150	0.145	0.140	0.141	0.142	0.145	0.151	0.167	0.161	0.143	0.148
89	*L. rowleyae*	0.134	0.126	0.126	0.133	0.125	0.138	0.132	0.133	0.128	0.119	0.128	0.132	0.134	0.126	0.134	0.126	0.131	0.153	0.169	0.148	0.173	0.142	0.145
90	*L. ardens*	0.128	0.128	0.130	0.134	0.128	0.143	0.138	0.132	0.130	0.120	0.122	0.130	0.133	0.130	0.133	0.133	0.131	0.153	0.164	0.139	0.152	0.126	0.145
91	*L. tuberosus*	0.107	0.116	0.106	0.119	0.120	0.128	0.126	0.107	0.112	0.110	0.118	0.107	0.120	0.116	0.118	0.122	0.133	0.141	0.140	0.124	0.142	0.124	0.123
92	*L. croceus*	0.144	0.136	0.130	0.150	0.140	0.142	0.142	0.132	0.132	0.122	0.149	0.122	0.141	0.122	0.116	0.126	0.114	0.135	0.170	0.149	0.171	0.140	0.144
93	*L. botsfordi*	0.126	0.120	0.119	0.136	0.126	0.136	0.128	0.128	0.124	0.114	0.124	0.120	0.118	0.108	0.112	0.122	0.126	0.126	0.145	0.130	0.151	0.119	0.131
94	*L. itiokai*	0.178	0.168	0.165	0.164	0.171	0.174	0.176	0.180	0.165	0.166	0.170	0.172	0.161	0.161	0.163	0.158	0.164	0.195	0.199	0.166	0.209	0.180	0.172
95	*L. parva*	0.186	0.161	0.180	0.143	0.175	0.191	0.162	0.164	0.184	0.168	0.177	0.167	0.166	0.188	0.176	0.186	0.181	0.213	0.172	0.176	0.189	0.159	0.143
96	*L. baluensis*	0.194	0.169	0.188	0.151	0.189	0.208	0.166	0.164	0.190	0.170	0.181	0.173	0.179	0.193	0.190	0.188	0.187	0.215	0.191	0.192	0.207	0.170	0.158
97	*L. brevicrus*	0.174	0.159	0.161	0.157	0.167	0.178	0.169	0.173	0.161	0.150	0.170	0.167	0.165	0.176	0.172	0.163	0.170	0.195	0.199	0.164	0.198	0.173	0.163
98	*L. mjobergi*	0.182	0.178	0.173	0.179	0.174	0.184	0.182	0.179	0.169	0.160	0.180	0.173	0.164	0.171	0.169	0.173	0.176	0.194	0.198	0.165	0.207	0.179	0.187
99	*L. juliandringi*	0.188	0.176	0.175	0.176	0.188	0.195	0.190	0.183	0.182	0.171	0.180	0.181	0.193	0.195	0.189	0.182	0.171	0.196	0.203	0.189	0.207	0.193	0.200
100	*L. fuliginosus*	0.165	0.140	0.167	0.151	0.185	0.191	0.149	0.152	0.176	0.142	0.160	0.143	0.164	0.180	0.167	0.178	0.168	0.189	0.165	0.170	0.174	0.141	0.147
101	*L. melanoleucus*	0.139	0.135	0.134	0.147	0.139	0.143	0.141	0.139	0.129	0.134	0.134	0.139	0.142	0.142	0.138	0.139	0.147	0.156	0.157	0.138	0.168	0.147	0.151
102	*L. sabahmontanus*	0.158	0.158	0.158	0.157	0.177	0.181	0.164	0.168	0.154	0.154	0.161	0.157	0.157	0.158	0.152	0.166	0.168	0.166	0.178	0.191	0.190	0.164	0.166
103	*L. dringi*	0.159	0.159	0.156	0.150	0.172	0.178	0.163	0.167	0.151	0.147	0.162	0.160	0.150	0.163	0.157	0.157	0.163	0.163	0.179	0.194	0.186	0.167	0.171
104	*L. pictus*	0.170	0.168	0.168	0.165	0.185	0.190	0.172	0.177	0.164	0.161	0.173	0.167	0.163	0.174	0.164	0.170	0.174	0.170	0.180	0.205	0.197	0.179	0.181
105	*L. fritinniens*	0.167	0.163	0.153	0.160	0.165	0.175	0.171	0.167	0.161	0.153	0.157	0.154	0.159	0.165	0.163	0.172	0.154	0.179	0.182	0.172	0.194	0.171	0.163
106	*L. hamidi*	0.164	0.145	0.152	0.158	0.175	0.181	0.155	0.156	0.158	0.153	0.159	0.150	0.147	0.163	0.148	0.161	0.151	0.166	0.172	0.193	0.174	0.160	0.163
107	*L. arayai*	0.160	0.151	0.149	0.150	0.157	0.167	0.149	0.156	0.150	0.149	0.155	0.152	0.147	0.156	0.150	0.158	0.147	0.160	0.175	0.193	0.177	0.149	0.159
108	*L. marmoratus*	0.158	0.154	0.150	0.154	0.167	0.175	0.159	0.154	0.146	0.145	0.151	0.146	0.155	0.160	0.148	0.163	0.153	0.151	0.167	0.191	0.184	0.156	0.157
109	*L. gracilis*	0.180	0.187	0.184	0.180	0.187	0.195	0.193	0.193	0.185	0.179	0.194	0.180	0.183	0.180	0.174	0.174	0.178	0.194	0.217	0.185	0.202	0.188	0.179
110	*L. maurus*	0.163	0.147	0.156	0.148	0.168	0.167	0.150	0.163	0.157	0.159	0.166	0.162	0.152	0.149	0.140	0.149	0.165	0.159	0.180	0.192	0.189	0.165	0.161
111	*L. solus*	0.192	0.194	0.190	0.198	0.196	0.209	0.196	0.192	0.189	0.187	0.189	0.192	0.200	0.203	0.191	0.195	0.191	0.200	0.224	0.198	0.232	0.200	0.193
112	*L. heteropus*	0.206	0.201	0.202	0.206	0.212	0.225	0.196	0.201	0.196	0.191	0.200	0.206	0.194	0.196	0.189	0.190	0.199	0.185	0.214	0.230	0.225	0.207	0.201
113	*L. kecil*	0.184	0.173	0.177	0.171	0.181	0.205	0.180	0.187	0.172	0.178	0.177	0.179	0.181	0.176	0.175	0.168	0.178	0.171	0.217	0.215	0.221	0.181	0.183
114	*L. kajangensis*	0.164	0.164	0.168	0.166	0.170	0.182	0.165	0.164	0.152	0.159	0.166	0.166	0.166	0.165	0.156	0.165	0.171	0.168	0.188	0.191	0.199	0.157	0.157
115	*Leptobrachium huashen*	0.207	0.204	0.197	0.212	0.199	0.205	0.215	0.213	0.205	0.206	0.218	0.208	0.206	0.203	0.199	0.198	0.187	0.217	0.248	0.229	0.246	0.210	0.217
116	*Megophrys glandulosa*	0.204	0.198	0.196	0.201	0.198	0.206	0.198	0.200	0.203	0.197	0.205	0.203	0.209	0.208	0.203	0.203	0.192	0.237	0.239	0.225	0.259	0.223	0.211

No.	Species	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
67	*L. sungi*	0.111
68	*L. zhangyapingi*	0.115	0.065
69	*L. isos*	0.126	0.123	0.121
70	*L. firthi*	0.132	0.121	0.127	0.110
71	*L. minimus*	0.094	0.085	0.095	0.114	0.123
72	*L. ventripunctatus*	0.098	0.097	0.099	0.115	0.115	0.068
73	*L. feii*	0.101	0.099	0.105	0.115	0.131	0.069	0.075
74	*L. aereus*	0.095	0.088	0.106	0.112	0.114	0.061	0.079	0.061
75	*L. wuhuangmontis*	0.108	0.100	0.114	0.114	0.127	0.086	0.093	0.087	0.075
76	*L. pluvialis*	0.087	0.082	0.092	0.120	0.117	0.055	0.067	0.071	0.051	0.081
77	*L. shangsiensis*	0.103	0.108	0.119	0.128	0.133	0.064	0.089	0.082	0.072	0.088	0.068
78	*L. nyx*	0.081	0.080	0.094	0.102	0.107	0.053	0.057	0.059	0.061	0.072	0.057	0.061
79	*L. nahangensis*	0.091	0.085	0.102	0.105	0.099	0.061	0.071	0.083	0.055	0.073	0.057	0.068	0.039
80	*L. kalonensis*	0.152	0.138	0.147	0.142	0.160	0.151	0.167	0.150	0.146	0.147	0.146	0.159	0.135	0.138
81	*L. bidoupensis*	0.137	0.120	0.142	0.129	0.154	0.140	0.158	0.144	0.129	0.130	0.137	0.155	0.130	0.132	0.051
82	*L. pallidus*	0.140	0.136	0.149	0.141	0.152	0.140	0.161	0.146	0.134	0.142	0.134	0.146	0.130	0.130	0.054	0.049
83	*L. tadungensis*	0.135	0.135	0.142	0.126	0.134	0.144	0.149	0.149	0.131	0.143	0.133	0.150	0.132	0.127	0.065	0.066	0.075
84	*L. macrops*	0.164	0.152	0.164	0.152	0.180	0.154	0.173	0.162	0.138	0.153	0.144	0.165	0.148	0.145	0.090	0.083	0.085	0.092
85	*L. pyrrhops*	0.151	0.154	0.157	0.142	0.161	0.163	0.156	0.163	0.142	0.154	0.151	0.158	0.145	0.141	0.088	0.089	0.084	0.081	0.110
86	*L. maculosus*	0.135	0.125	0.128	0.136	0.144	0.143	0.141	0.139	0.123	0.133	0.131	0.152	0.125	0.126	0.073	0.074	0.081	0.073	0.094	0.075
87	*L. melicus*	0.134	0.130	0.136	0.130	0.134	0.130	0.134	0.122	0.103	0.128	0.122	0.139	0.112	0.110	0.092	0.078	0.091	0.090	0.116	0.113	0.079
88	*L. applebyi*	0.138	0.138	0.138	0.128	0.144	0.141	0.151	0.146	0.132	0.141	0.132	0.159	0.131	0.136	0.100	0.084	0.093	0.096	0.125	0.122	0.088	0.058
89	*L. rowleyae*	0.136	0.142	0.150	0.150	0.150	0.137	0.141	0.135	0.113	0.129	0.125	0.160	0.125	0.126	0.098	0.101	0.090	0.089	0.121	0.104	0.083	0.065	0.087
90	*L. ardens*	0.129	0.130	0.140	0.129	0.145	0.128	0.144	0.126	0.116	0.120	0.127	0.142	0.121	0.122	0.082	0.082	0.076	0.078	0.100	0.085	0.057	0.047	0.068	0.066
91	*L. tuberosus*	0.104	0.119	0.123	0.106	0.135	0.117	0.115	0.103	0.106	0.111	0.114	0.123	0.101	0.103	0.114	0.103	0.106	0.103	0.131	0.107	0.105	0.107	0.124	0.117	0.097
92	*L. croceus*	0.133	0.128	0.134	0.135	0.141	0.127	0.129	0.128	0.102	0.124	0.121	0.150	0.122	0.112	0.111	0.105	0.115	0.110	0.142	0.124	0.120	0.098	0.119	0.110	0.098
93	*L. botsfordi*	0.114	0.111	0.120	0.125	0.124	0.111	0.113	0.113	0.100	0.114	0.108	0.123	0.096	0.089	0.125	0.107	0.115	0.108	0.154	0.124	0.108	0.098	0.111	0.116	0.092
94	*L. itiokai*	0.165	0.159	0.161	0.167	0.165	0.154	0.168	0.150	0.149	0.158	0.157	0.174	0.153	0.143	0.172	0.166	0.161	0.164	0.178	0.190	0.153	0.147	0.147	0.155	0.155
95	*L. parva*	0.148	0.132	0.148	0.172	0.183	0.178	0.146	0.136	0.144	0.178	0.134	0.181	0.171	0.138	0.184	0.151	0.181	0.180	0.173	0.198	0.168	0.169	0.169	0.152	0.134
96	*L. baluensis*	0.165	0.144	0.157	0.184	0.189	0.188	0.161	0.159	0.154	0.183	0.147	0.186	0.177	0.147	0.181	0.147	0.179	0.176	0.166	0.186	0.172	0.167	0.173	0.148	0.134
97	*L. brevicrus*	0.170	0.161	0.172	0.174	0.176	0.170	0.172	0.166	0.160	0.182	0.164	0.181	0.162	0.161	0.179	0.171	0.172	0.175	0.181	0.182	0.167	0.149	0.165	0.159	0.152
98	*L. mjobergi*	0.165	0.164	0.167	0.169	0.171	0.164	0.176	0.169	0.151	0.170	0.174	0.178	0.161	0.149	0.167	0.156	0.165	0.163	0.175	0.156	0.159	0.155	0.169	0.163	0.152
99	*L. juliandringi*	0.178	0.183	0.185	0.187	0.194	0.176	0.176	0.174	0.175	0.192	0.176	0.176	0.174	0.162	0.168	0.161	0.161	0.171	0.181	0.166	0.165	0.144	0.152	0.159	0.156
100	*L. fuliginosus*	0.122	0.129	0.133	0.155	0.194	0.159	0.143	0.133	0.125	0.147	0.126	0.172	0.148	0.113	0.158	0.113	0.151	0.159	0.144	0.173	0.157	0.145	0.145	0.116	0.098
101	*L. melanoleucus*	0.136	0.139	0.139	0.151	0.150	0.126	0.157	0.151	0.125	0.129	0.130	0.141	0.123	0.110	0.141	0.125	0.136	0.136	0.154	0.151	0.133	0.125	0.119	0.132	0.112
102	*L. sabahmontanus*	0.163	0.158	0.165	0.159	0.152	0.143	0.153	0.172	0.143	0.156	0.148	0.162	0.142	0.131	0.135	0.140	0.140	0.135	0.156	0.162	0.143	0.127	0.124	0.134	0.139
103	*L. dringi*	0.160	0.159	0.169	0.161	0.153	0.148	0.150	0.165	0.147	0.159	0.147	0.165	0.141	0.132	0.138	0.147	0.147	0.138	0.167	0.159	0.146	0.136	0.142	0.144	0.149
104	*L. pictus*	0.175	0.166	0.173	0.166	0.158	0.157	0.161	0.178	0.149	0.164	0.154	0.168	0.141	0.140	0.151	0.158	0.155	0.148	0.171	0.168	0.157	0.143	0.145	0.145	0.151
105	*L. fritinniens*	0.153	0.157	0.166	0.161	0.163	0.156	0.154	0.160	0.142	0.152	0.147	0.162	0.146	0.140	0.151	0.142	0.152	0.134	0.167	0.162	0.157	0.145	0.145	0.142	0.146
106	*L. hamidi*	0.157	0.160	0.157	0.139	0.160	0.143	0.153	0.157	0.145	0.154	0.158	0.157	0.146	0.135	0.153	0.150	0.152	0.154	0.173	0.170	0.162	0.128	0.130	0.136	0.140
107	*L. arayai*	0.152	0.160	0.165	0.135	0.160	0.147	0.163	0.159	0.147	0.144	0.158	0.164	0.146	0.145	0.147	0.146	0.144	0.152	0.166	0.166	0.151	0.128	0.122	0.136	0.129
108	*L. marmoratus*	0.159	0.147	0.149	0.143	0.146	0.147	0.149	0.159	0.143	0.142	0.148	0.164	0.142	0.133	0.147	0.148	0.148	0.143	0.169	0.166	0.151	0.126	0.118	0.130	0.131
109	*L. gracilis*	0.169	0.178	0.182	0.180	0.188	0.176	0.188	0.184	0.163	0.180	0.177	0.193	0.178	0.170	0.175	0.167	0.161	0.171	0.182	0.168	0.173	0.157	0.164	0.173	0.157
110	*L. maurus*	0.152	0.138	0.152	0.139	0.156	0.145	0.165	0.154	0.137	0.149	0.156	0.167	0.139	0.140	0.166	0.152	0.155	0.152	0.163	0.175	0.152	0.137	0.133	0.149	0.139
111	*L. solus*	0.180	0.184	0.185	0.176	0.198	0.173	0.189	0.179	0.162	0.168	0.175	0.196	0.180	0.163	0.188	0.169	0.174	0.171	0.202	0.168	0.171	0.174	0.164	0.186	0.161
112	*L. heteropus*	0.187	0.185	0.187	0.177	0.203	0.160	0.188	0.176	0.171	0.177	0.173	0.178	0.167	0.172	0.186	0.170	0.181	0.171	0.216	0.171	0.184	0.162	0.160	0.181	0.170
113	*L. kecil*	0.166	0.175	0.174	0.153	0.197	0.157	0.190	0.174	0.167	0.160	0.173	0.189	0.163	0.164	0.175	0.160	0.162	0.167	0.200	0.171	0.169	0.150	0.150	0.173	0.149
114	*L. kajangensis*	0.142	0.153	0.155	0.139	0.156	0.141	0.165	0.149	0.133	0.140	0.146	0.169	0.144	0.139	0.153	0.136	0.150	0.133	0.173	0.149	0.143	0.138	0.130	0.159	0.121
115	*Leptobrachium huashen*	0.210	0.205	0.216	0.197	0.215	0.202	0.205	0.202	0.193	0.202	0.200	0.228	0.190	0.180	0.214	0.218	0.209	0.207	0.240	0.201	0.198	0.201	0.203	0.201	0.199
116	*Megophrys glandulosa*	0.212	0.198	0.207	0.191	0.202	0.203	0.198	0.193	0.187	0.179	0.201	0.223	0.187	0.198	0.205	0.204	0.209	0.200	0.229	0.219	0.196	0.192	0.190	0.195	0.184

No.	Species	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115
92	*L. croceus*	0.100
93	*L. botsfordi*	0.078	0.098
94	*L. itiokai*	0.152	0.151	0.153
95	*L. parva*	0.134	0.143	0.133	0.055
96	*L. baluensis*	0.140	0.139	0.145	0.096	0.061
97	*L. brevicrus*	0.164	0.155	0.155	0.100	0.082	0.082
98	*L. mjobergi*	0.141	0.143	0.128	0.129	0.114	0.116	0.116
99	*L. juliandringi*	0.156	0.152	0.163	0.127	0.127	0.123	0.127	0.127
100	*L. fuliginosus*	0.100	0.113	0.099	0.166	0.191	0.195	0.180	0.181	0.170
101	*L. melanoleucus*	0.121	0.123	0.113	0.148	0.147	0.143	0.162	0.163	0.158	0.067
102	*L. sabahmontanus*	0.136	0.138	0.136	0.150	0.177	0.181	0.164	0.167	0.172	0.154	0.129
103	*L. dringi*	0.135	0.133	0.135	0.156	0.172	0.172	0.153	0.157	0.159	0.176	0.138	0.056
104	*L. pictus*	0.145	0.143	0.147	0.161	0.183	0.179	0.159	0.172	0.175	0.170	0.146	0.040	0.060
105	*L. fritinniens*	0.134	0.145	0.137	0.153	0.143	0.151	0.164	0.157	0.168	0.131	0.131	0.064	0.076	0.056
106	*L. hamidi*	0.136	0.130	0.138	0.154	0.182	0.178	0.161	0.153	0.158	0.165	0.137	0.085	0.102	0.094	0.087
107	*L. arayai*	0.134	0.136	0.138	0.149	0.175	0.167	0.175	0.156	0.165	0.167	0.135	0.094	0.108	0.104	0.095	0.052
108	*L. marmoratus*	0.127	0.130	0.126	0.145	0.171	0.171	0.166	0.153	0.160	0.165	0.133	0.081	0.094	0.090	0.085	0.044	0.040
109	*L. gracilis*	0.153	0.157	0.173	0.184	0.167	0.163	0.175	0.177	0.179	0.156	0.161	0.116	0.116	0.120	0.116	0.107	0.103	0.105
110	*L. maurus*	0.139	0.135	0.150	0.144	0.166	0.180	0.158	0.166	0.169	0.167	0.128	0.085	0.100	0.100	0.105	0.083	0.088	0.077	0.099
111	*L. solus*	0.163	0.157	0.169	0.189	0.163	0.163	0.195	0.187	0.199	0.150	0.168	0.177	0.178	0.179	0.180	0.175	0.175	0.169	0.181	0.164
112	*L. heteropus*	0.170	0.172	0.174	0.193	0.208	0.202	0.202	0.194	0.192	0.189	0.175	0.189	0.174	0.174	0.183	0.166	0.182	0.170	0.195	0.173	0.064
113	*L. kecil*	0.170	0.165	0.165	0.194	0.195	0.195	0.191	0.195	0.193	0.176	0.162	0.180	0.181	0.188	0.180	0.174	0.170	0.174	0.182	0.154	0.100	0.112
114	*L. kajangensis*	0.132	0.130	0.126	0.165	0.176	0.181	0.178	0.164	0.162	0.155	0.134	0.139	0.157	0.152	0.147	0.133	0.131	0.119	0.144	0.113	0.115	0.133	0.122
115	*Leptobrachium huashen*	0.197	0.201	0.189	0.210	0.208	0.211	0.219	0.198	0.230	0.234	0.187	0.214	0.201	0.214	0.214	0.208	0.200	0.204	0.223	0.199	0.221	0.234	0.216	0.204
116	*Megophrys glandulosa*	0.188	0.204	0.200	0.196	0.198	0.196	0.200	0.199	0.215	0.228	0.190	0.197	0.200	0.200	0.196	0.187	0.185	0.185	0.203	0.180	0.208	0.204	0.229	0.205	0.190

Table S4 Call properties of *Leptobrachella* yeae sp. nov. and *L. oshanensis*.

Species	Vouncher	Call type and number	Dominant frequency (Hz)	Call duration (ms)	Call interval (ms)	1st note pulses	2nd note pulses	3rd note pulses	4th note pulses	1st note interval	2nd note interval	3rd note intervals	Note rise time (ms)	Harmonic 1 (Hz)	Harmonic 2 (Hz)	Harmonic 3 (Hz)
Leptobrachella yeae sp. nov.	CIBEMS20190422HLJ2-1	A, $n = 6$	4562.5 ± 139.8	70.3 ± 12.2	2488 ± 1268.3	7.2 ± 1.1	/	/	/	/	/	/	29.7 ± 15.2	9000.0 ± 530.3, $n = 6$	14437.5 ± 187.5, $n = 2$	/
Leptobrachella yeae sp. nov.	CIBEMS20190422HLJ2-1	E, $n = 10$	4575.0 ± 150.0	347.4 ± 60.2	1224.9 ± 510.6	31.3 ± 6.7	/	/	/	/	/	/	41.6 ± 28.3	9150.0 ± 343.7, $n = 10$	14250 ± 265.2, $n = 4$	/
Leptobrachella yeae sp. nov.	CIBEMS20190422HLJ1-6	E, $n = 21$	4946.4 ± 147.3	668.5 ± 47.5	200.4 ± 20.4	40.5 ± 2.9	/	/	/	/	/	/	59.2 ± 12.8	9750.0 ± 0.0, $n = 21$	/	/
Leptobrachella yeae sp. nov.	CIBSSC17127	E, $n = 20$	4706.3 ± 186.6	404.7 ± 67.6	591.8 ± 229	27.3 ± 6.3	/	/	/	/	/	/	57.5 ± 20.5	8678.6 ± 397.3, $n = 14$	/	/
Leptobrachella yeae sp. nov.	CIBSSC17128	E, $n = 21$	4875.0 ± 0.0	695.7 ± 156.2	221.4 ± 38.7	37.4 ± 7.9	/	/	/	/	/	/	71.0 ± 14.8	9164.1 ± 577.4, $n = 16$	/	/
Leptobrachella yeae sp. nov.	CIBEM1839	E, $n = 21$	4875.0 ± 0.0	505.8 ± 56.6	181.0 ± 67.4	38.0 ± 5.5	/	/	/	/	/	/	80.0 ± 73.3	/	/	/
Leptobrachella yeae sp. nov.	CIBEM1840	E, $n = 20$	4875.0 ± 0.0	534.7 ± 57.3	161.1 ± 14.8	27.3 ± 3.2	/	/	/	/	/	/	53.4 ± 10	/	/	/
L. oshanensis	CIBEMS20190421BGS5	A, $n = 20$	4500.0 ± 0.0	38.7 ± 15.4	1629.5 ± 659.1	7.4 ± 2.7	/	/	/	/	/	/	3.0 ± 0.7	8362.5 ± 582.2, $n = 20$	13012.5 ± 171.8, $n = 20$	/
L. oshanensis	CIBEMS20190421BGS5	B, $n = 10$	4462.5 ± 112.5	115.8 ± 13.3	218.1 ± 188.2	3.7 ± 1.6	5.9 ± 1.8	/	/	40.6 ± 14.9	/	/	76.1 ± 12.7	7350.0 ± 417.6, $n = 10$	12600.0 ± 343.7, $n = 10$	/
L. oshanensis	CIBEMS20190421BGS5	C, $n = 12$	4343.8 ± 184.9	282.3 ± 15.0	253.6 ± 48.1	4.5 ± 1.3	30.8 ± 6	/	/	23.7 ± 14.9	/	/	72.4 ± 14	8156.3 ± 346.6, $n = 12$	12718.8 ± 284.7, $n = 12$	/
L. oshanensis	CIBEMS20190421BGS5	D, $n = 20$	4500.0 ± 0.0	317.2 ± 32.0	130.8 ± 45.1	4.1 ± 0.7	5.2 ± 1.9	4.4 ± 1.5	7.5 ± 2.2	37.2 ± 7.6	34.8 ± 17.1	44.5 ± 14.1	262.3 ± 32.1	8400.0 ± 248.7, $n = 20$	12806.3 ± 463.5, $n = 20$	/
L. oshanensis	CIBEMS20190421BGS5	E, $n = 9$	4291.7 ± 186.3	318.7 ± 40.6	1595.6 ± 1950.3	62.6 ± 8.9	/	/	/	/	/	/	34.7 ± 79.3	8416.7 ± 186.3, $n = 9$	12500.0 ± 353.6, $n = 9$	/
L. oshanensis	CIBEMS20190421BGS6	B, $n = 13$	4384.6 ± 173.1	138.1 ± 13.8	152.5 ± 34.5	6.6 ± 1.9	13.2 ± 3	/	/	29.2 ± 13.2	/	/	82.7 ± 8.4	8480.8 ± 182.4, $n = 13$	12750.0 ± 375, $n = 2$	/
L. oshanensis	CIBEMS20190421BGS6	E, $n = 19$	4184.2 ± 136.7	213.9 ± 53.8	1627.1 ± 940.9	48.5 ± 10.7	/	/	/	/	/	/	47.2 ± 41.6	8291.7 ± 393.1, $n = 18$	12468.8 ± 310.9, $n = 8$	/
L. oshanensis	CIBEMS20190421BGS7	A, $n = 21$	4142.9 ± 79.9	53.5 ± 7.4	1562.0 ± 700.2	6.1 ± 1.2	/	/	/	/	/	/	2.1 ± 0.3	8506.6 ± 212.6, $n = 19$	12812.5 ± 400.2, $n = 6$	/
L. oshanensis	CIBEMS20190421BGS7	B, $n = 20$	4237.5 ± 171.8	133.7 ± 18.5	153.6 ± 8.1	2.2 ± 0.5	3.1 ± 0.2	/	/	74.3 ± 19.3	/	/	100.1 ± 16.2	8512.5 ± 692.5, $n = 20$	12712.5 ± 201.9, $n = 20$	/
L. oshanensis	CIBEMS20190421BGS7	E, $n = 5$	4200.0 ± 150.0	231.8 ± 15.3	2809.2 ± 2776.2	34.4 ± 3.9	/	/	/	/	/	/	7.6 ± 9.7	8325.0 ± 280.6, $n = 5$	12525.0 ± 450.0, $n = 5$	/
L. oshanensis	CIBEMS20190421SSG1-8	B, $n = 25$	4425.0 ± 150.0	145.9 ± 24.4	232.5 ± 112.9	2.8 ± 0.6	3.0 ± 0.7	/	/	68.2 ± 16.8	/	/	109.5 ± 18.8	8355.0 ± 168.4, $n = 25$	12562.5 ± 324.8, $n = 16$	/
L. oshanensis	CIBEMS20190421SSG1-8	C, $n = 20$	4462.5 ± 163.5	279.1 ± 29.2	266.6 ± 134.7	3.1 ± 0.5	25.2 ± 5.8	/	/	43.8 ± 12.1	/	/	77.6 ± 10.3	8493.8 ± 341.1, $n = 20$	12937.5 ± 187.5, $n = 2$	/
L. oshanensis	CIBEMS20190421SSG1-8	D, $n = 20$	4462.5 ± 112.5	264.9 ± 46.9	132.3 ± 16.7	2.6 ± 0.5	2.4 ± 0.5	2.3 ± 0.5	2.5 ± 1.4	49.5 ± 14.8	49.5 ± 12.6	47.5 ± 26	86.3 ± 8.9	8606.3 ± 81.7, $n = 20$	13531.3 ± 582.1, $n = 12$	/
L. oshanensis	CIBEMS20190421SSG1-8	E, $n = 5$	4275.0 ± 183.7	308.2 ± 15.4	476.0 ± 38.8	44.0 ± 2.4	/	/	/	/	/	/	96.2 ± 84.1	8100.0± 183.7, $n = 5$	12093.8 ± 162.4, $n = 4$	15000 ± 0, $n = 4$
L. oshanensis	CIBEMS20190422SSG4-1	A, $n = 6$	4000.0 ± 176.8	53.7 ± 6.0	1040.3 ± 438.7	6.0 ± 0.8	/	/	/	/	/	/	2.7 ± 0.7	7812.5 ± 455, $n = 6$	12062.5 ± 139.8, $n = 6$	/
L. oshanensis	CIBEMS20190422SSG4-1	C, $n = 10$	4275.0 ± 183.7	202.5 ± 21.4	214.0 ± 196.6	2.1 ± 0.3	19.4 ± 2.8	/	/	27.0 ± 4.5	/	/	52.5 ± 3.5	8062.5 ± 345.7, $n = 10$	12000.0 ± 375.0, $n = 10$	/
L. oshanensis	CIBEMS20190422SSG4-1	E, $n = 5$	4050.0 ± 150.0	220.4 ± 17.7	745.8 ± 441.1	32.8 ± 3.2	/	/	/	/	/	/	94.8 ± 90.7	7650.0 ± 300.0, $n = 5$	12000.0 ± 0.0, $n = 5$	/

Note: "/" for missing data